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THE ACOUSTIC SIGNATURE OF GAS-BEARING SEDIMENTS IN TWO COASTAL INLETS OF ATLANTIC CANADA

P.E. KEPKAY and R.C. COOKE

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The effect of free gas on the reflectivity of recently deposited muds in 2 Nova Scotian inlets is modelled using in situ measurements of acoustic velocity and the calculated effect of interstitial methane bubbles on bulk density.

Velocity profiles of the gas-bearing sediments show that a relatively small (2.5%) velocity contrast between gassy muds overlying substantially less gassy muds coincides with an acoustic reflector apparent on seismic profiles from the 2 inlets.

Reflection coefficients calculated at vertical incidence show that a sub-bottom reflector twice as reflective as the sediment-water interface is controlled primarily by a density contrast between gas-bearing muds and substantially gas-free muds rather than by any large velocity contrast.

Introduction

The Atlantic coast of Nova Scotia is indented by inlets resulting from the flooding of ice-modified valleys following deglaciation (Piper & Keen 1976). Recently deposited muds in 2 such inlets, Halifax Harbour and St. Margaret's Bay (Fig 1) have been examined to explain the way in which interstitial free gas is associated with a strong sub-bottom acoustic reflector apparent on profiler records.

Echo sounder and sparker profiles of St. Margaret's Bay muds in 50 to 70 m of water show a prominent sub-bottom acoustic reflector; Keen and Piper (1976) have stated that it is caused by free gas rather than by lithological changes within the sediment, and that it is a sufficiently strong acoustic barrier to prevent penetration by relatively low-powered, high-frequency sources. Comparable reflectors have been mapped in the same distance sub-bottom at a variety of hydrostatic pressures, ie., in water depths ranging from 24 to 30 m in Halifax Harbour (N.S. Dept. Develop. 1975) down to 70 m in Mahone Bay (Barnes 1976). Reflectors similar in appearance have been reported in numerous coastal environments, such as Chesapeake Bay (Schubel 1974), the Norwegian Channel (Van Weering et al. 1973) and coastal areas of the North Sea (Rawson 1976).

As Keen and Piper (1976) have described, the reflector is restricted to fine-grained sediments in St. Margaret's Bay and varies between 1.8 and 4.0 m below the flat-lying mud floors of 2 basins. The reflector downdips sharply either at basin margins or where a sub-bottom high (till or bedrock) nearly reaches the sediment surface. The general characteristics of the reflector in Halifax Harbour are the same (Fig 2), and it is confined to regions of ponded deposition. However, the downdipping ter-

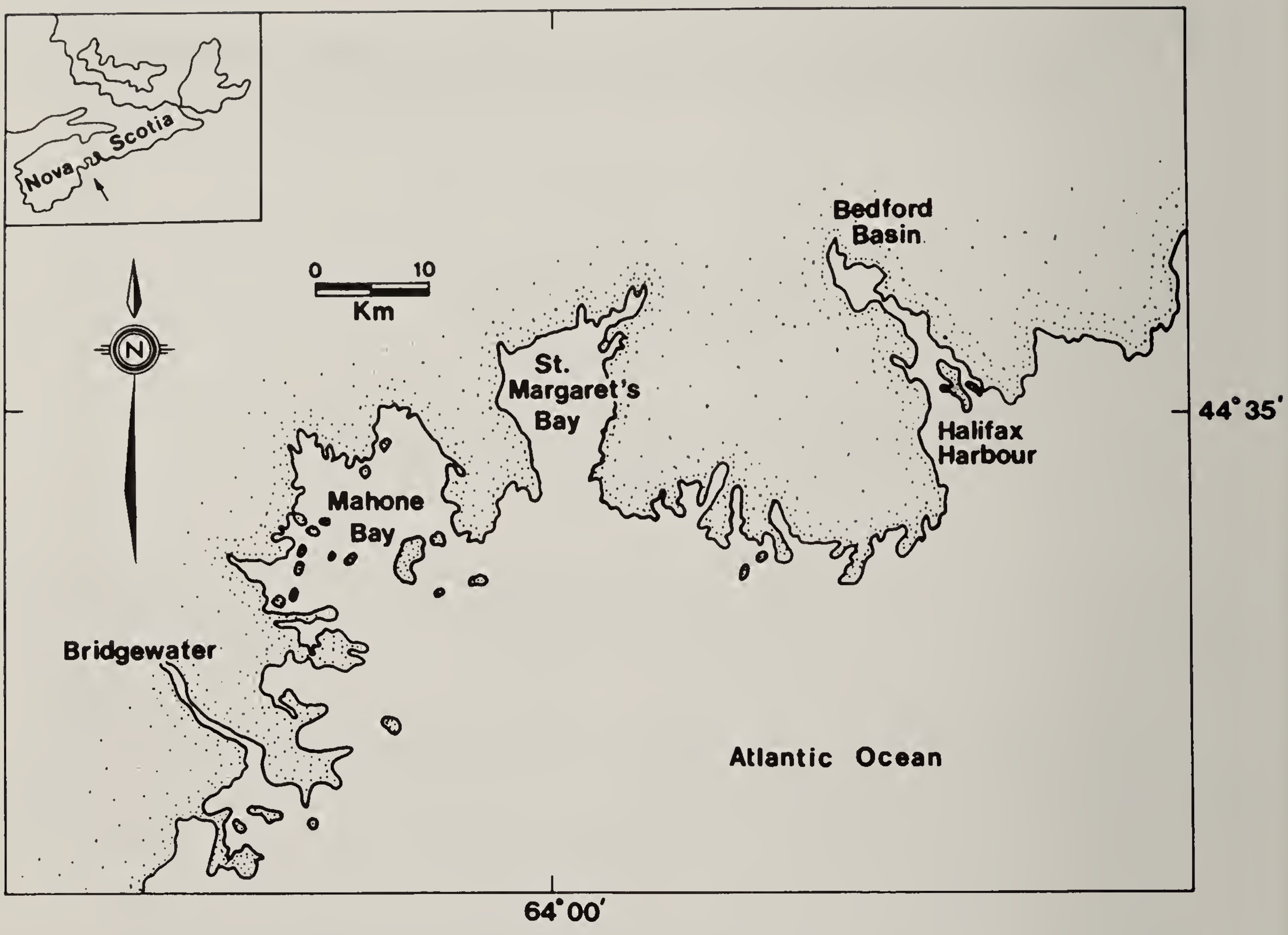

Fig 1. Location of the study areas on the Atlantic coast of Nova Scotia.

mination of the reflector in Halifax Harbour is not always associated with topography, sub-bottom or otherwise (Fig 2).

The appearance of the reflector depends on the type of acoustic source used. It shows up as an impenetrable acoustic mask on 3.5 kHz transducer systems (Fig 2a). The signature on sparker records (Fig 2b) is more akin to the "acoustically turbid zones" of Schubel (1974), although use of a sufficiently powerful source of lower frequency can penetrate the reflector (Piper & Keen 1976).

From the analysis of a 10 m piston core, Keen and Piper (1976) have shown that methane is associated with the reflector, generating large expansion voids at 1 to 2 m sub-bottom in the core when it is brought to the surface. In anoxic marine sediments, carbon dioxide is microbially reduced to methane below a horizon dominated by sulfate-reducing bacteria (Claypool & Kaplan 1974).A microbial origin for methane is probable when evidence from the St. Margaret's Bay sediments is considered; data of Keen and Piper (1976) show a downward decrease of organic carbon in cores to about one-half the surface value at the depth of the reflector (about 2 m), and the methane found in the St. Margaret's Bay sediments is not associated with its higher homologs (Rashid & Vilks, in press), indicating that the gas has not leaked from petroleum accumulations. Rashid and Vilks (in press) also measured markedly less sulfate in cores of gassy sediment compared with cores collected from gas-free environments, indicating a microbial succession leading to methane production.

We report here, from sound velocity profiles determined in situ, how interstitial methane bubbles in the fine-grained sediments of Halifax Harbour and St. Margaret's Bay act to produce a sub-bottom acoustic reflector.

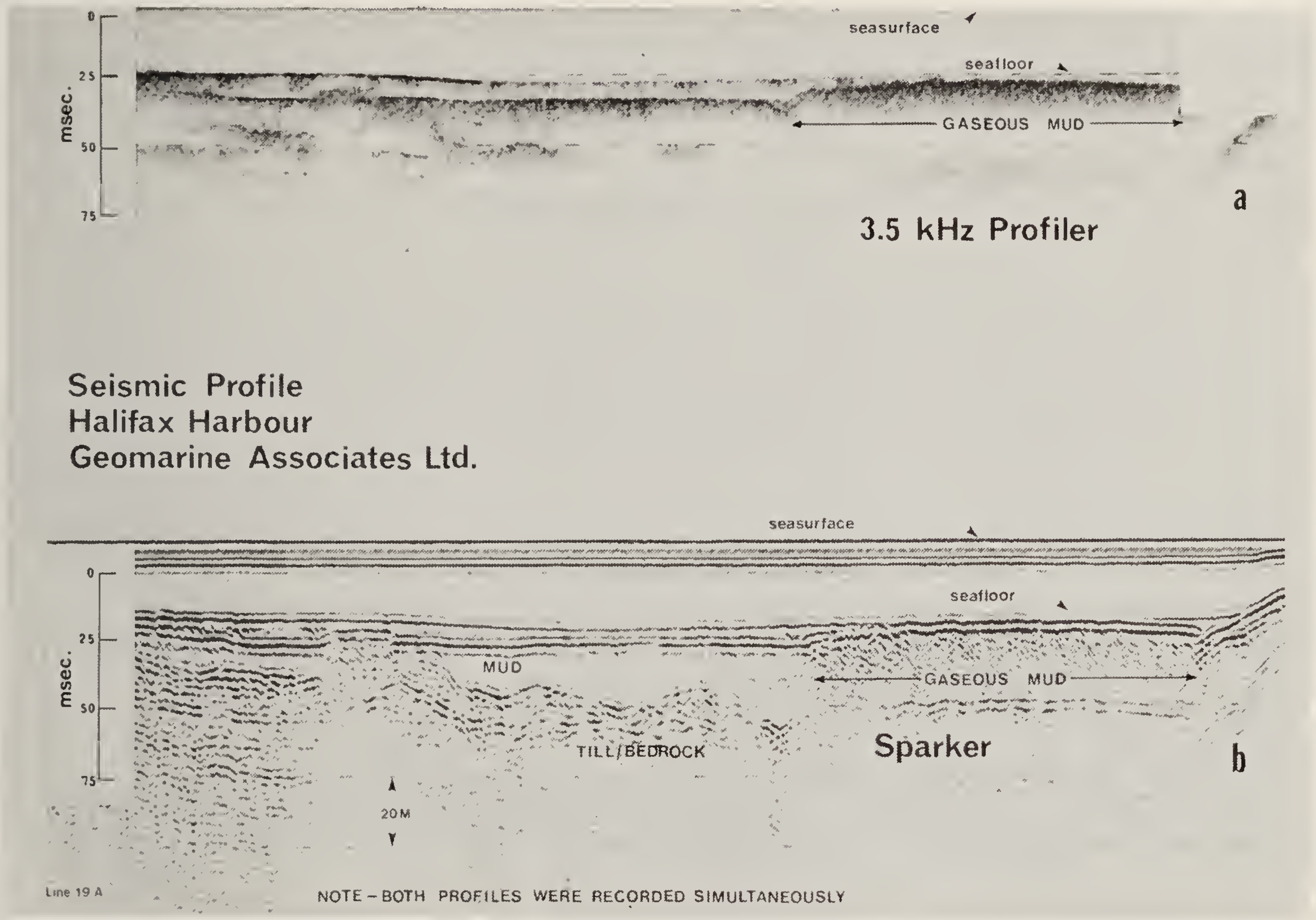

Fig 2. Simultaneous 3.5 KHz transducer (2a) and lower frequency sparker (2b) profiles showing the reflector as an acoustic mask in Halifax Harbour (courtesy of Geomarine Associates, Halifax). The two-way travel time is shown in milliseconds and the vertical scale in meters is based on the speed of sound in seawater. The sub-bottom reflectance cannot be quantitatively compared to that of the sea floor on these profiles.

Controls of Reflectivity

Two factors must be considered to describe the reflectivity of gas-bearing sediments. Most commonly examined is the redirection of sound (much of it back to a surface receiver) due to the scattering effect of resonating bubbles. In addition, the effect of interstitial free gas on sound velocity and acoustic impedance determines the reflection coefficients at interfaces between gas-bearing and gas-free sediments.

Bubble Resonance

Minnaert's (1933) equation for the resonant frequency of bubbles in water subject to an underwater sound source is:

$$\mathrm{fr} = \frac{1}{2\pi r_o} \left(\frac{3\gamma P_o}{\varrho_w}\right)^{1/2}$$

where fr is the fundamental pulsation in Hz; r, the bubble radius;γ, the ratio of the specific heat of the gas at constant volume to the specific heat at constant pressure; P_o, the hydrostatic pressure; and ϱ_w, the water density. Explicit in the equation is the inverse relationship between the frequency of sound applied and the radius of a bubble capable of resonating. The basic expression has been modified by Andreeva (1964) to include the elastic properties of a solid so that:

$$fr = \frac{1}{2\pi r_o}\left(\frac{3\gamma P_o + 4G}{\varrho_s}\right)^{1/2}$$

where ϱ_s is the solid density and G, the elastic shear modulus of the solid.

If sound with a frequency range of 1 to 15 kHz is applied, bubbles ranging from 7583 μm down to 506 μm diameter would be required to establish resonance, when $\gamma = 1.30$ (for methane; International Critical Tables), $G = 10^6$ dynes/cm^2 (Anderson 1974) $\varrho_o = 1.01 \times 10^6$ dynes and $\varrho_s = 1.42$ g/cm^3 (for a wet silty clay; Hamilton 1976). The largest interstitial bubbles that Kepkay and Cooke (1978) observed in laboratory muds of the same grain size were 60 μm diameter. It is clear then that the interstitial bubbles found in sediments of the type associated with the acoustic reflectors in Halifax Harbour and St. Margaret's Bay will not resonate and scatter the sound incident from even high frequency transducer sources.

Changing Acoustic Impedance

The reflection coefficient as the ratio of reflected to incident amplitudes of a plane wavefront at a flat-lying elastic boundary is:

$$r = \frac{\varrho_2 v_2 - \varrho_1 v_1}{\varrho_2 v_2 + \varrho_1 v_1}$$

for the case of vertical incidence. The products of the bulk densities and sound velocities, $\varrho_i v_i$ [i = 1, 2], are the acoustic impedances above and below the boundary.

It is generally assumed in the case of gassy sediments that low sound velocity is the dominant control of their acoustic impedance. Wood's (1931) emulsion theory predicts this velocity behavior because of the effect of only small numbers of evenly dispersed bubbles on the bulk modulus of the system (Anderson 1974). However, Domenico (1976) and Kepkay and Cooke (1978) have shown in the laboratory that this is not the case in natural sediments containing less than 20% by volume of free gas because interstitial bubbles do not behave as an emulsion. Therefore, to define the reflectivity of the gas-bearing sediments in Halifax Harbour and St. Margaret's Bay, the in situ measurement of acoustic velocities was carried out and the effect of free gas on wet sediment density was determined.

Velocity Probe

Design and Operation

The probe is based on Schubel's (1974) method of monitoring the pulse driving a transmitter on one leg and the acoustic signal picked up by a receiver on the other. In our design, the delay time between transmission and reception of compressional waves was recorded employing the delay facility of an oscilloscope connected to the single-cylinder, piezo-electric elements of hydrophones free to slide in the legs. The probe and time delay system is described in more detail by Kepkay (1977). The received signal was filtered passing 3 to 100 kHz, so that the acoustic wavelengths used were all greater than 1 cm in seawater and the frequency range encompassed those employed in high resolution profiler systems.

The acoustic velocity profiles of the gas-bearing sediments in Halifax Harbour and St. Margaret's Bay were determined along with the velocity profile of a gas-free mud in Bedford Basin. The travel time of sound in seawater was determined at each site before the probe was allowed to free-fall into the sediment. The salinity and temperature of the seawater at each site were obtained (Jordan 1972; El Din et al. 1970) and used to calculate the sound velocity from Wilson's (1960) equation. Thus, with the acoustic velocity and travel time in seawater, the correct travel path between transmitter and receiver could be calculated at each site. This distance was then used rather than the separation of the probe legs to compute acoustic velocities from travel times measured in the sediments. Probe penetration was recorded to within 5 cm by mud adherence to scales on the legs and delay times were recorded at a series of sub-bottom depths by reeling in or letting out the hydrophones together.

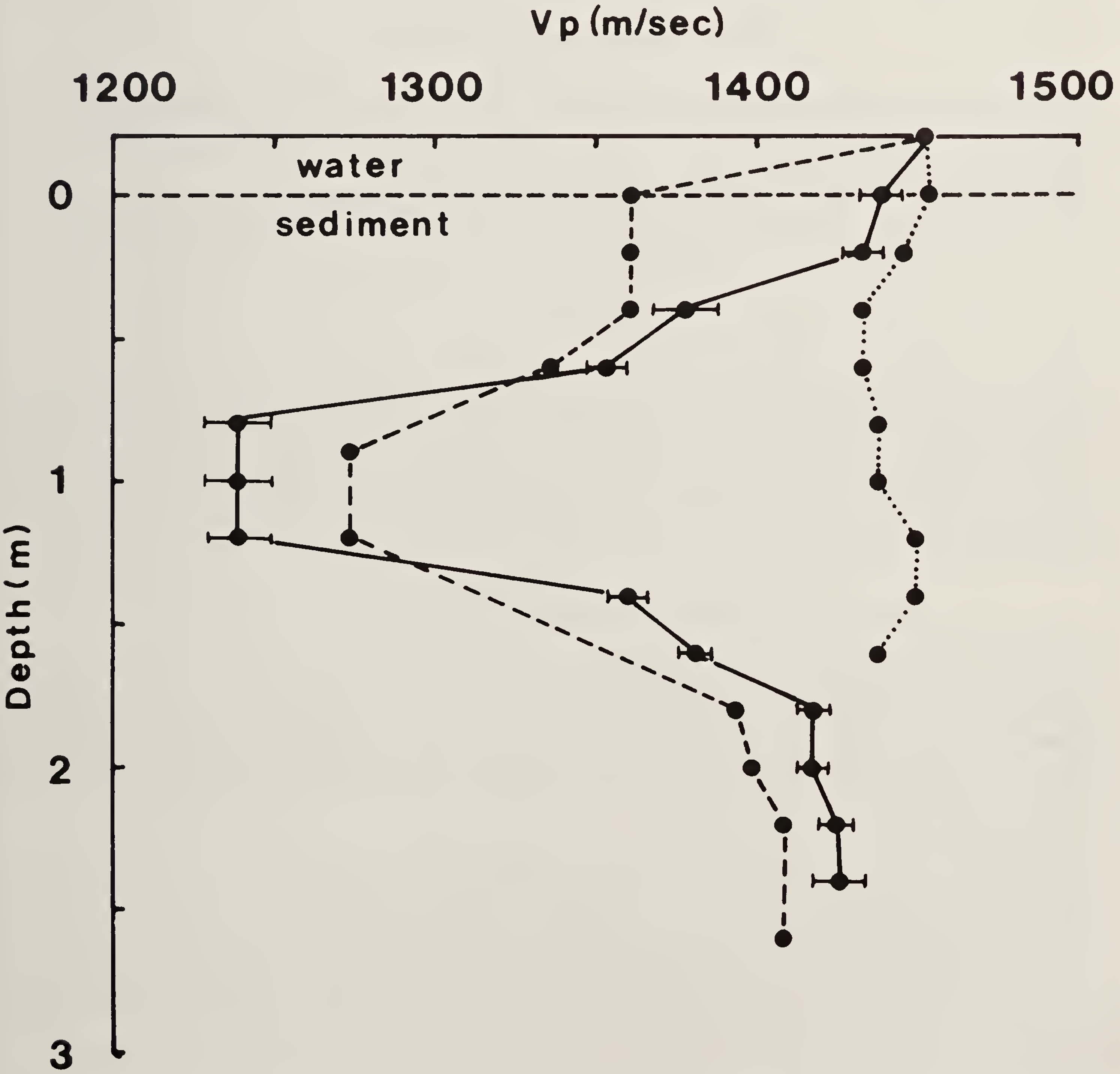

Fig. 3 Velocity(V_p) profiles through gas horizons in Halifax Harbour (•—•) and St. Margaret's Bay (•–•) muds. Profiles at a gas-free control site in Bedford Basin (•...•) are shown for comparison, and the velocity of sound in seawater is shown as a reference. Mean sediment velocities were calculated from 5 profiles taken at the same site in Halifax Harbour, and the error bars delineate 2 times the standard deviation.

Discussion of Results

Figure 3 shows compressional velocity profiles from sites in Halifax Harbour and St. Margaret's Bay where the reflector was recorded at 1.85 m sub-bottom on profiler records, and from the control area in Bedford Basin. The general vertical pattern of velocities measured in the 2 gas-bearing sediments is the same for reflectors at the same depth sub-bottom and significantly different from the sequences measured at the control site.

The acoustic reflector at an apparent sub-bottom depth of 1.85 m on profiler records of the gas-bearing sediments (corrected to 1.73 m using the measured sediment velocities) is coincident with a downward transition to a higher acoustic velocity. This relationship, which is also implicit in Schubel's (1974) measurements of signal loss in the gassy sediments of Chesapeake Bay, must form the basis for any model of the reflector in both areas.

Bulk Density Determinations

Wet sediment densities were calculated from the weight fractions of silty clay and water in diver-collected cores from Halifax Harbour so that decreasing water content with increasing burial was taken into account.

The weight fractions of pore water and dry sediment were converted to volume fractions using the density of Halifax Harbour bottom water (1.03 g/cm^3) and that of silty clay (2.70 g/cm^3) from Hamilton's (1976) synthesis of world marine sediment data. The bulk densities of gas-free sediment were then calculated by dividing total weight by total volume fractions. The estimated gas volumes associated with specific velocities in the Halifax Harbour profile were obtained from the laboratory data of Kepkay and Cooke (1978) and converted to weight fractions using the density of methane at 0°C and 2 m sub-bottom in Halifax Harbour (0.02 g/cm^3, assuming ideal gas behavior). The weight and volume fractions of gas were then incorporated in the calculation of the bulk densities of gassy sediment, assuming that gas replaces water.

Models of Gas-Zone Reflectivity

Calculation of Reflection Coefficients

To determine reflection coefficients from equation 3, interfaces must be defined between distinct layers of different acoustic impedance. Therefore, stepped profiles (Fig 4) were drawn through the velocity and bulk density data from Halifax Harbour, so that six imaginary interfaces were defined between the sediment surface and 2 m sub-bottom.

Kepkay and Cooke (1978) have shown in the laboratory that a significant volume of gas can accumulate with no apparent velocity decrease. This requires the derivation of at least 2 distinct models of acoustic impedance (models A and B in Fig 4) in addition to a model assuming no gas (model C). The 2 models differ only in the upper 0.2 m which can have a bulk density equivalent of 3.2% gas by volume (model A) or 13.8% gas by volume (model B).

Discussion of Reflectivity Models

As Figure 4 shows, model B (high gas content in the upper 0.2 m) satisfies 2 qualitative observations from transducer and sparker records. First, the most reflective interface (with a calculated reflection coefficient of 0.10) is 1.8 m sub-bottom. Second, low reflectivity (with a calculated reflection coefficient of 0.05) is evident at the sediment-water interface. Both models A and B, using gassy sediment den-

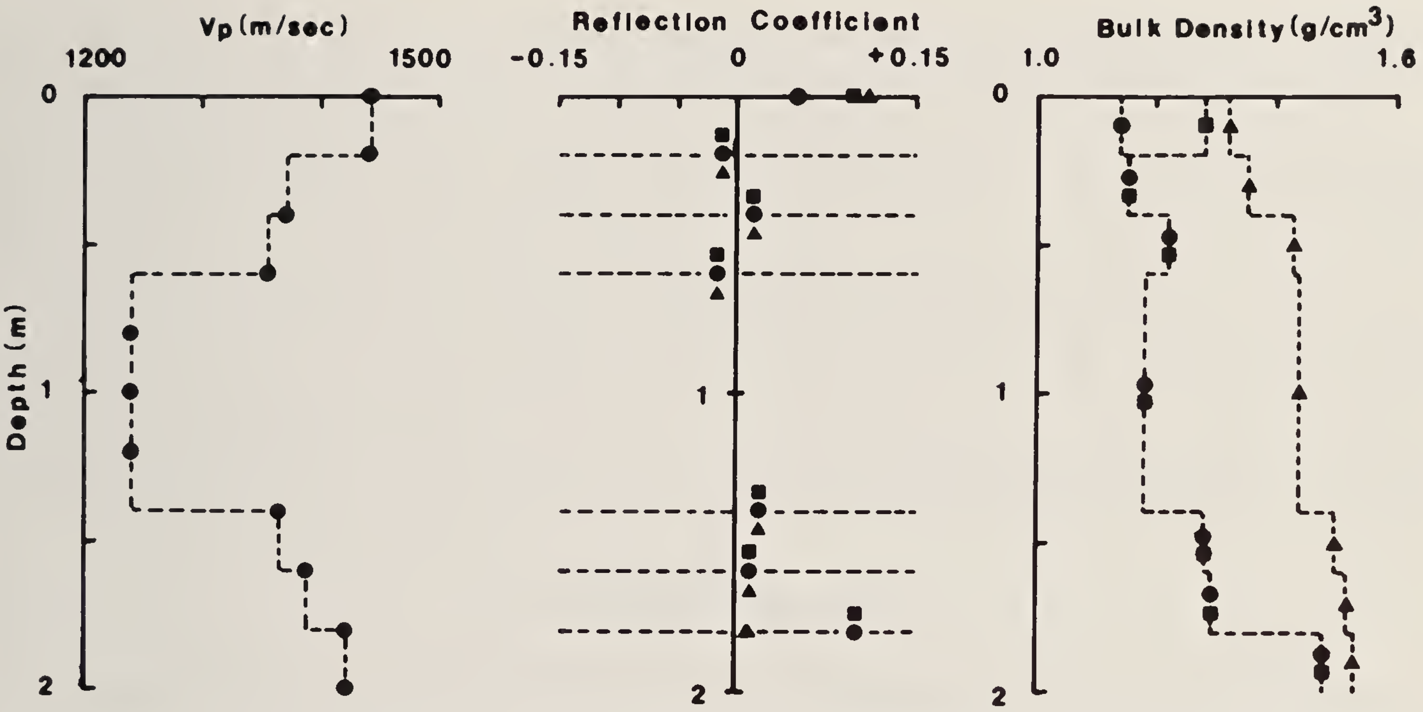

Fig 4. Reflection coefficients calculated at 6 sub-bottom interfaces generated by a step profile of acoustic velocity through Halifax Harbour data and 3 bulk density profiles. Models A (■) and B (●) use gassy sediment densities and only differ in the free gas content of the upper 0.2 m of sediment. The densities of Model C (▲) are calculated assuming no free gas, so that only velocity contrasts are involved in the control of reflectivity.

sities, show that it is possible to develop a reflective interface at 1.8 m sub-bottom between a less dense zone of gas-rich sediment overlying a denser, almost gas-free sediment. Model C, without free gas, shows high reflectivity (0.10) at the sediment-water interface and low reflectivity (0.02) at the 1.8 m interface. This emphasizes the importance of the gas-control of bulk density in producing a reflector at this depth, and shows that an acoustic velocity contrast alone is not sufficient to produce the reflector recorded.

The reason for a relatively low bulk density yet no velocity reduction in the upper 0.2 m may be that bubble populations are unevenly distributed, as described by Kepkay and Cooke (1978). More even distributions may exist below, unable to migrate through undisturbed sediment (Kepkay & Cooke, unpubl. data) and it is not difficult to imagine bioturbation or the disturbance of sediment by currents contributing to an uneven bubble distribution in the top 0.2 m.

The conclusion that a downward decrease in gas concentration controls sub-bottom reflectivity is in apparent conflict with Rashid and Vilks' (in press) data, which show an increasing methane content with increasing depth in a 9 m piston core from the St. Margaret's Bay muds. However, the absence of dissolved gas data from sub-bottom horizons equivalent to where velocity increases to a relatively high value at 1.8 m could mean that this conflict is indeed apparent. Their data allow the existence of a low-gas zone over a sub-bottom depth interval of 1.8 to 2.4 m that, in turn, may be underlain by other gas bodies. Schubel (1974) has already suggested that gas-bearing sediments in Chesapeake Bay with similar acoustic signatures could be vertically interlayered with virtually gas-free zones less than 1 m thick.

Although the reflectivity models show that a reflector at 1.8 m can be twice as reflective as the sediment-water interface (model B), the absolute value of the reflection coefficient is low (i.e., the maximum possible reflected amplitude is 10% of the incident). However, these values are within the ranges measured for marine sediments by Akal (1974), and agree with the qualitative impression of reflectance conveyed by the seismic profiles in Figure 2.

Although our modelling of reflectivity at vertical incidence is overly simplistic, it demonstrates that acoustic velocity contrasts need not be the major control of reflectivity at an interface between gas-bearing and gas-free sediments. More complex models that do not assume vertical incidence may be required, and it must be stressed that the density control of reflectivity in gassy muds described in this work cannot be applied to all gas-bearing sediments. At present, the factors controlling the implied free gas distributions are being examined, and it is clear that future work in these highly accessible nearshore areas should include the examination of the physical controls of bubble populations in situ for a correct understanding of the acoustics of gas-bearing sediments.

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GROWTH, HARVEST AND SURVIVAL OF HATCHERY-REARED AND NATIVE BROOK TROUT (SALVELINUS FONTINALIS) IN THE DUNK RIVER SYSTEM, PRINCE EDWARD ISLAND

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Brook trout *(Salvelinus fontinalis)* were studied over 4 years in the coastal Lower Dunk River, the freshwater Scales Pond, and the small, inland Upper Dunk River in Prince Edward Island. Length and weight increments for hatchery brook trout in the Lower and Upper Dunk River areas during the first 120 days after release were significantly greater than those of tagged native trout in the same areas. In the Lower Dunk River, annual growth increments were greater for hatchery trout than for tagged or untagged native trout, but did not differ in the 2 kinds of trout in the Upper Dunk River, where hatchery trout grew significantly more slowly than they did downstream. Better growth of both kinds of brook trout in the Lower Dunk River than in the Upper Dunk River was related to food and trout densities. Summer harvests of hatchery trout were similar in the Lower Dunk River and Scales Pond, ranging from 9.1-30% of those released. Summer harvests of tagged native brook trout in the Lower Dunk River were never greater than 10%. Harvests of hatchery trout in the Upper Dunk River were usually lower than in the other areas. It was estimated that 32% of the hatchery trout were still present in the Lower Dunk River by July but only 8% by mid-August. Only 0.2-1% of the hatchery trout released were recovered the next year and none more than 1.5 yr after release, whereas 1-2.1% of the tagged native brook trout were recovered the next year. Larger trout at tagging were captured more frequently immediately following release and less frequently later in the season. Trout captured after more than 100 d after release were generally the smaller trout at tagging. The effects of food, trout densities, predation movement, and weather on growth and harvest of hatchery trout together with their effect on the Dunk River sport fishery are discussed.

Introduction

Hatchery-reared brook trout Salvelinus fontinalis have been released annually to Prince Edward Island streams and ponds as supplements to wild populations. Such releases are assumed to improve trout production and to enhance sport fishing, but there is little documented evidence to support this assumption. Only Smith (1957), Saunders and Smith (1964), Smith and Saunders (1968), and White (1927; 1930) have reported on the fate of hatchery brook trout in waters of Prince Edward Island. The present 4-year study (1972 to 1975) was undertaken (a) to describe the growth, harvest and survival of a domesticated strain of hatchery-reared brook trout released as yearlings to different regions of the Dunk River system; (b) to compare these data where possible with those from native brook trout cohabiting the same regions of the system and finally (c) to consider the management implications of these findings.

Description of the Dunk River System

The Dunk River system (Fig 1), 46°21'N, 63°36'W, is one of Prince Edward Island's larger river systems situated in the midst of a highly developed agricultural region. It is easily accessible by many roads and paths, and is only a short distance from either Summerside or Charlottetown. As a result, it is among the most heavily fished systems on Prince Edward Island.

Along the river system, a riparian growth of alder *(Alnus rugosa),* white spruce *(Picea glauca),* balsam fir *(Abies balsamea),* trembling aspen *(Populus tremuloides),*

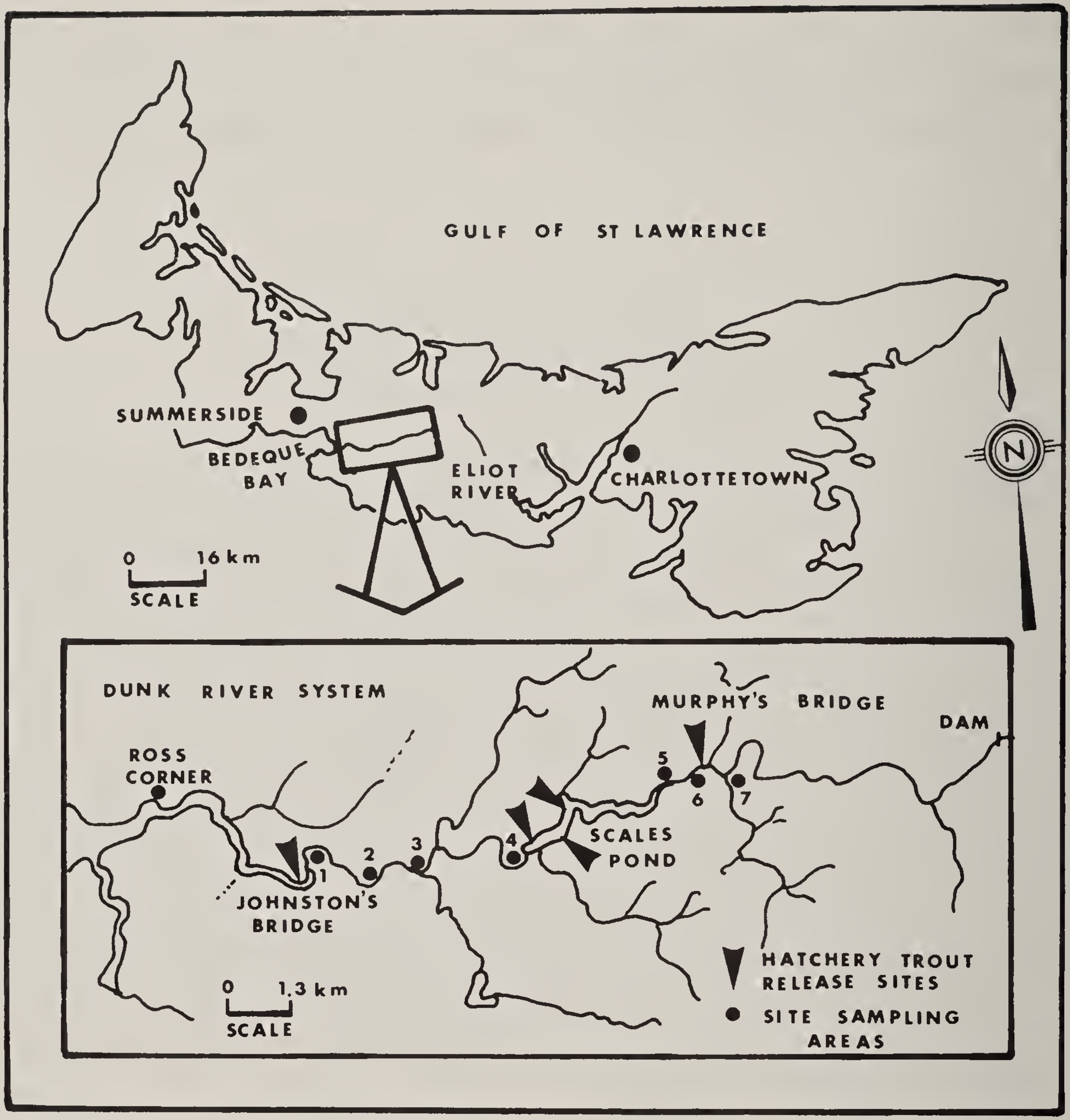

Fig 1. The Dunk River system on Prince Edward Island.

eastern hemlock *(Tsuga canadensis),* white birch *(Betula papyrifera),* beech *(Fagus grandifolia)* and sugar maple *(Acer saccharum)* is frequently broken by cultivated fields or pasture land. Fertilizers applied to the fields frequently wash into the river during heavy rains, making it highly productive (Stewart & Himelman 1974). The water chemistry of this system has been described already by Johnston and McKenna (1976).

The study of hatchery and native brook trout was carried out in three different regions. The Lower Dunk River extends from the bridge at Ross Corner, 13 km inland, to the dam at Scales Pond which is an impassable barrier to the upriver movement of trout and other fish species. Below the dam, the river is 8.0 to 17.0 m wide and 0.1 to 1.3 m deep, and has a surface area of 10.4 ha during summer. Shallow pools (<0.6 m) form 30% of the water area while runs (0.6-1.0 m), deep pools (>0.6 m) and riffles (<0.3 m) constituted 26%, 24%, and 20% respectively. A slight rise and fall of water during tidal cycles was observed 0.5 km above Johnston's Bridge.

Fish species observed in the Lower Dunk River include brook trout *Salvelinus fontinalis),* rainbow trout *(Salmo gairdneri),* Atlantic salmon *(Salmo salar),* American eel *(Anguilla rostrata),* and 3-spine stickleback *(Gasterosteus aculeatus).* Smelts *(Osmerus mordax)* and gaspereau *(Alosa pseudoharengus)* are seasonal migrants, spawning in the river each year between April and July.

The second region, Scales Pond, is a body of fresh water with a surface area of 23.5 ha and a length of 3.0 km. Most of the pond is shallow with a mean summer depth of 2.0 m and a maximum depth of 4.4 m. In summer, the surface water varies between 15°C and 25°C, and in some areas the bottom is 3 to 6°C cooler because of springs and ground water seepage. The only fish in the pond are brook trout, rainbow trout and 3-spine stickleback.

The third region, a section of the Upper Dunk River, runs 7 km from the head of Scales Pond to a second impassable dam at Breadalbane. This section is narrow, shallow, and shaded by overhanging alder and other shade trees. Brook trout, rainbow trout, and 3-spine stickleback are the only fish species present.

Methods

Stocking Program for Hatchery Brook Trout

Hatchery brook trout used in the study were reared from eggs of domesticated hatchery stock cultured at the Cardigan Fish Culture Station in eastern Prince Edward Island. Yearlings were weighed, measured for fork length, and jaw-tagged during May. In late May or early June of each year, approximately 1000 hatchery trout were released at Johnston's Bridge in the Lower Dunk River, 1500 in Scales Pond, and 1000 at Murphy's Bridge in the Upper Dunk River (Fig 1). Growth and recovery information for each group was obtained through river sampling and creel census programs.

Tagging of Native Brook Trout

In early June of each year, native brook trout similar in size to the introduced hatchery trout were captured in 4 selected sites of the Lower Dunk River and in 3 sites of the Upper Dunk River (Fig 1), by electrofishing and seining. They were weighed, measured for fork length, jaw-tagged, and released.

Scale Analysis

Native brook trout were sampled for scales throughout the study period, and age and length determinations were made from scale readings and measurements. Lengths were calculated by using the following equation:

$$\text{Log } L = 5.81 + 0.947 \log S \, (r = 0.87)$$

where L represents fork length (mm) to be calculated and S anterior scale measurement (mm).

River Sampling

Data on the growth of hatchery and native brook trout following release were obtained by recapturing trout at 4 sites on the Lower Dunk River and at 3 sites on the Upper Dunk River at approximately 20-day intervals between June and September. Recaptured trout were measured for fork length, weighed, and then released.

Angling Returns

Information about tagged trout was obtained from fishermen through a voluntary tag-return program. A tag-draw incentive was used in 1972 and 1973, but in 1974 and 1975 was replaced with a cash settlement of 25¢ per tag.

Creel Census

Information on the growth and harvest of tagged hatchery and native brook trout was also obtained through a creel survey of fishermen angling on the Lower Dunk River and Scales Pond. The survey was conducted each year between May 7 and

Sept. 3, 1973-75, which includes the period of greatest fishing pressure. While angling pressure is usually great on opening day (Apr. 15) and on the first few weekends after opening day, most of the fishing pressure occurs during May, June and July. Therefore, angling data in the first 22 days or the last 27 days (Sept. 3-30) of the fishing season were obtained from voluntary returns.

The creel census was stratified into 30-day strata, into weekdays and weekend days, and into a.m. and p.m. periods. The interval for each a.m. was from 0700 to 1300 and for each p.m. from 1300 until darkness. For every 5 weekdays, 3 a.m. and 3 p.m. periods were sampled and for every 2 weekend days, 1 a.m. and 1 p.m. period were sampled. The periods to be sampled each week were randomly selected and all holidays were considered as weekdays.

Two creel census clerks interviewed all fishermen encountered in the Lower Dunk River and Scales Pond areas. At least 2 or 3 complete surveys of each area per a.m. or p.m. period were made, depending on day length. Incomplete and complete fishing trips were used in the harvest estimate calculations.

The total harvest by fishermen for the period from May 7 to Sept. 3, was calculated from the estimated harvests for weekdays a.m., weekdays p.m., weekend days a.m. and weekend days p.m. for each 30-day stratum. The estimated harvest for each was calculated from the estimated hours fished and the mean catch per hour. Stratum totals were then summed to provide the harvest total for each census year.

Population Estimates

During 1973 and 1974, several population assessments were made by electrofishing the Lower Dunk River to determine the number of tagged hatchery and native trout alive. Approximately 13-15% of each water type (i.e., run, riffle, shallow and deep pool) in the Lower Dunk River was sampled. The estimated number of hatchery and native trout in each area sampled was determined using the Zippin (1958) method with a minimum of 3 complete fishings per area. An estimate for the total area was then made.

Results and Discussion

Growth

To demonstrate that a comparison of growth increments for recaptured hatchery and native brook trout was valid, the sizes at tagging of the recaptured trout (Table I) were compared statistically by an analysis of covariance. No significant differences between hatchery and native brook trout stocks could be demonstrated that would invalidate the comparisons.

The changes in mean fork length and weight of tagged hatchery trout between June and the end of September in the Lower Dunk River were 6 to 7 cm (Fig 2) and 60 to 80 g (Fig 3), respectively. In comparison, growth of tagged native brook trout of a similar size as hatchery trout at release was 4 to 5 cm and 20 to 40 g. When the length increments for 0 to 120 days for the two groups were compared statistically using a *t*-test, growth of hatchery trout was significantly greater ($P<0.01$) than that of native trout. Weight increments of hatchery trout were also significantly greater ($P<0.01$). Only 4 hatchery trout were caught 367 to 416 days after tagging; they grew an average of 10.5 cm and 158.7 g. Eighteen tagged native brook trout were caught 340 to 420 days after tagging and they grew an average of 7.3 cm and 108.1 g.

Annual growth increments in length for 127 untagged native brook trout as calculated from scale readings were 5.7 cm for trout aged 1 to 2 yr and 7.8 for trout aged 2 to 3 yr (Fig 4). Although the size of native brook trout in the 2 age groups was within the range of lengths for hatchery trout, their average annual length increment

Table I. Summary of fork lengths (cm), fresh weights (g), and coefficients of condition at tagging for hatchery and native brook trout used in the growth comparisons.

	Lower Dunk River		Scales Pond	Upper Dunk River	
	Hatchery brook trout	Native brook trout	Hatchery brook trout	Hatchery brook trout	Native brook trout
Number of trout tagged	360	978	435	207	1071
Range of fork lengths at tagging	10.1-20.9	8.6-21.8	10.1-21.3	10.8-19.2	8.5-18.2
Mean fork length	14.8	14.2	14.6	15.2	11.5
Range of fresh weights at tagging	12.1-126.4	8.3-147.3	8.0-123.6	13.4-110.0	3.8-78.2
Mean fresh weight	48.1	42.9	43.5	53.6	17.5
Range of coefficient of condition at tagging	0.88-2.30	0.90-2.37	0.64-2.13	1.03-2.06	0.33-2.22
Mean coefficient of condition	1.39	1.37	1.36	1.46	1.09

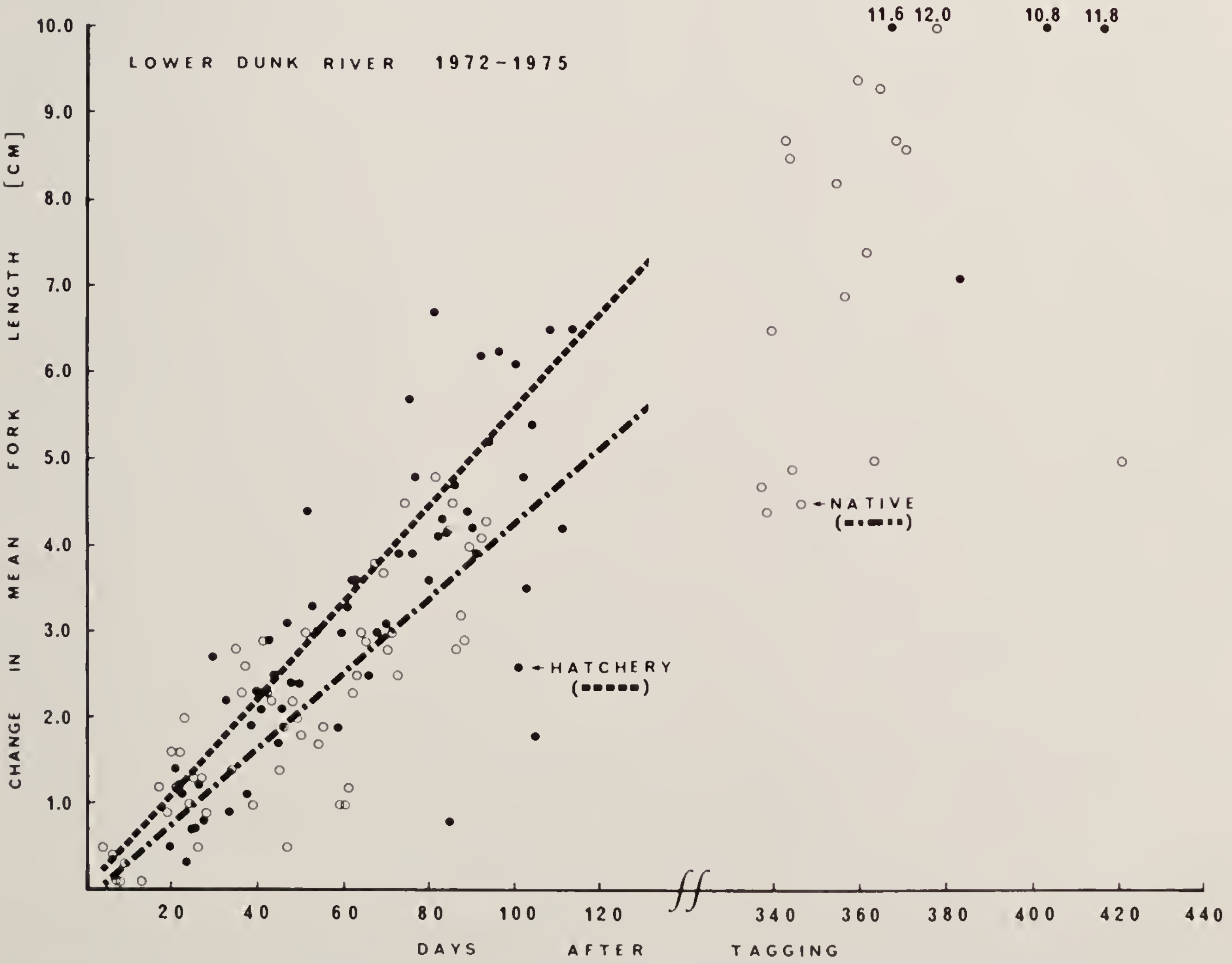

Fig 2. Changes in length of brook trout following tagging in the Lower Dunk River.

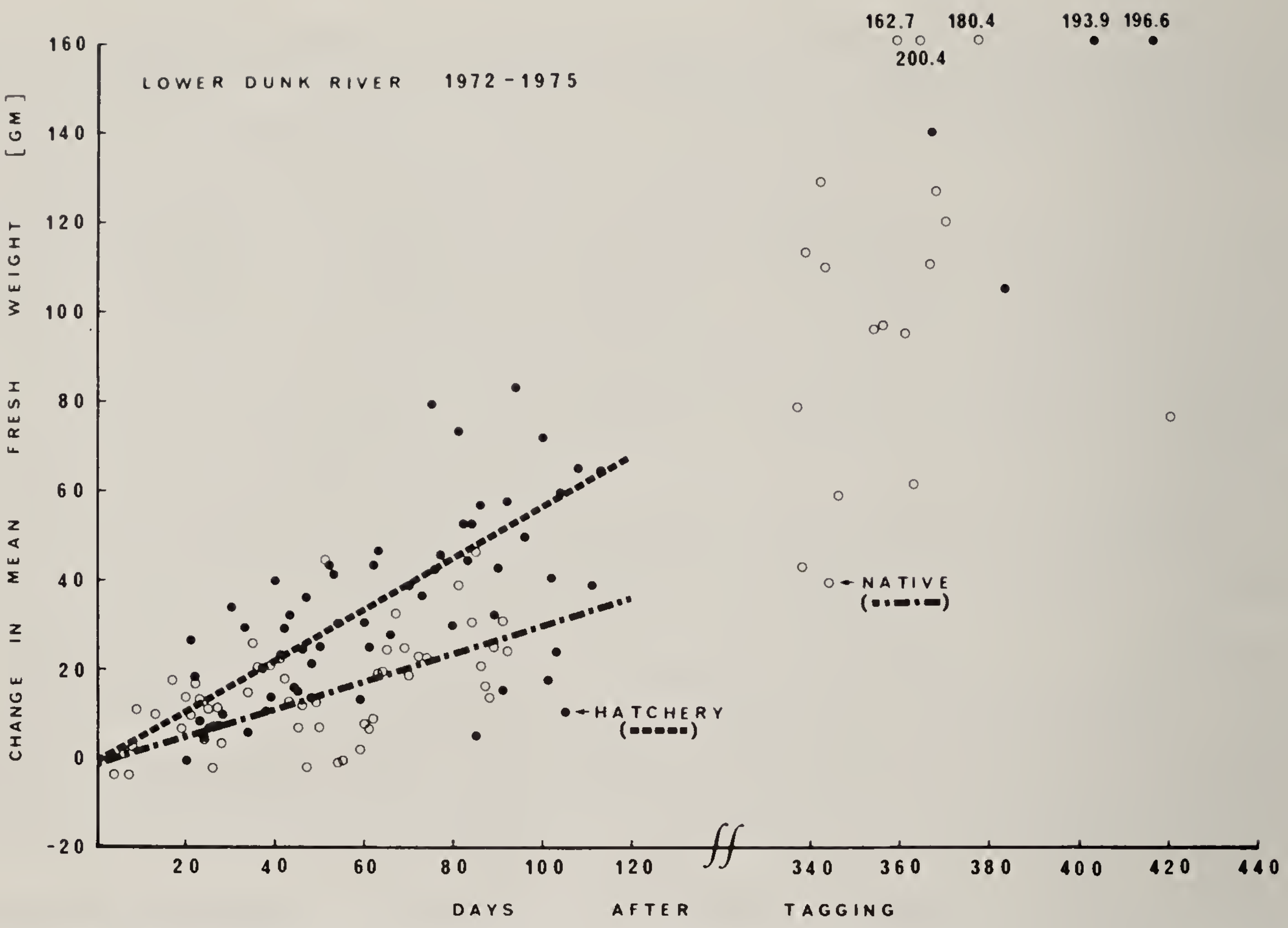

Fig 3. Changes in weight of brook trout following tagging in the Lower Dunk River.

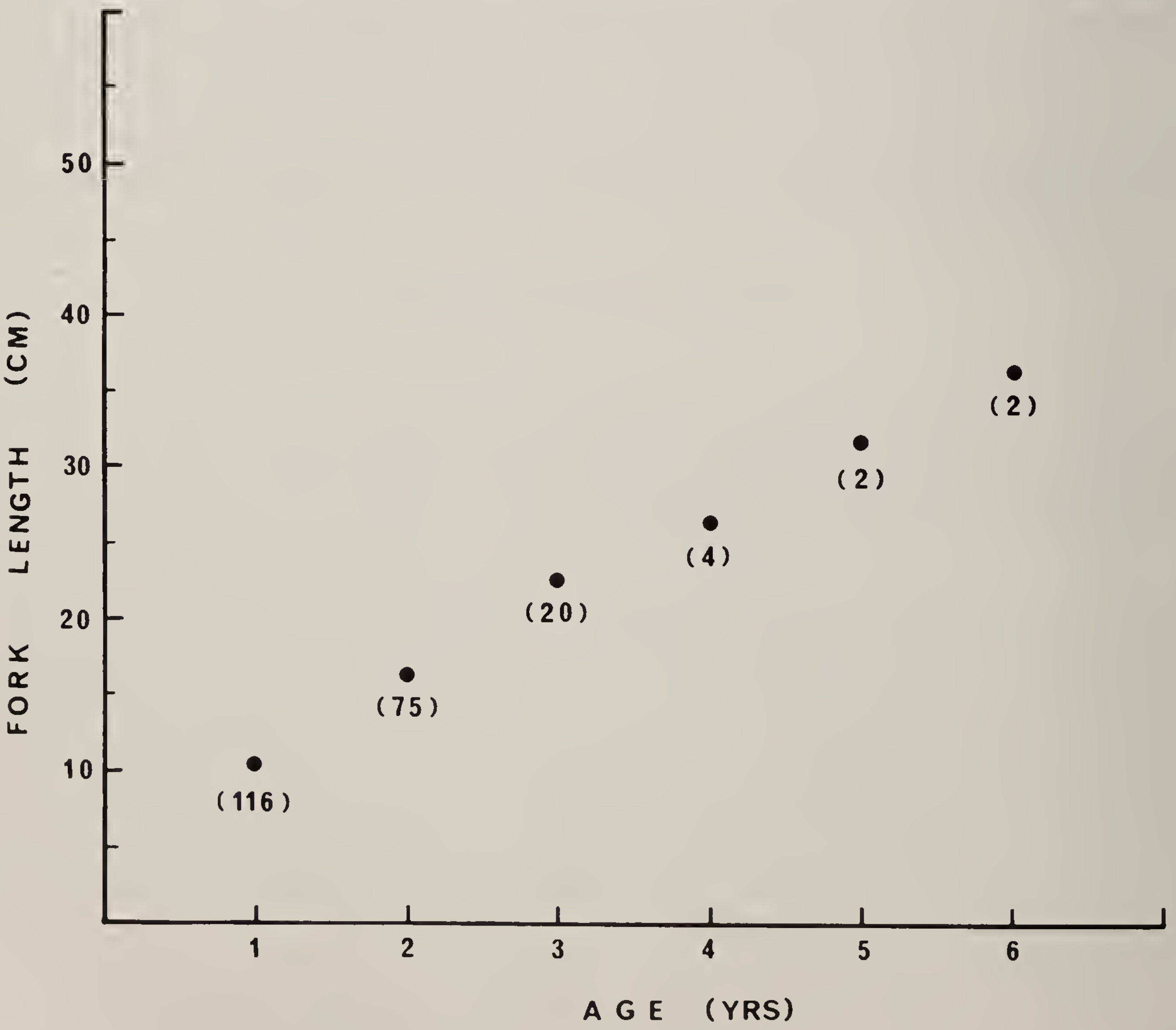

Fig 4. Size of untagged native brook trout at different ages in the Lower Dunk River as determined by scale analysis. Each point represents a mean value; the sample size for each point is in parentheses.

(6.7 cm) was markedly lower than that for tagged hatchery trout (10.5 cm), but similar to that for tagged native trout (7.3 cm).

Both hatchery and wild brook trout experienced some decline in condition after release. Data indicate that nearly 50% of the hatchery trout sampled in the first 100 days in the Lower Dunk River showed a loss in condition (Fig 5). The extent of condition decline was generally greater for tagged native brook trout than for tagged hatchery trout. While losses in condition were common for both groups during the first summer following release, some improvement in condition occurred by the next spring.

In Scales Pond, 5961 hatchery trout were released and 435 were later recaptured and used in the growth study. Attempts to capture large numbers of native brook trout similar in size to the hatchery trout in Scales Pond failed. Of those tagged, only 2 were recaptured later in the season. As a result, no comparative information is presented for native brook trout in this area.

Changes in mean length and weight of hatchery trout in Scales Pond during the summer were 5 to 6 cm (Fig 6) and 50 to 60 g (Fig 7). Weight and length increases were compared by *t*-test with weight and length increments for hatchery trout in the Lower Dunk River and were not significantly different. Only one hatchery trout in Scales Pond was reported surviving more than 1 year after release, and this trout grew 3.6 cm and 30.4 g.

Losses in condition factor were also evident for hatchery trout from Scales Pond (Fig 8). Such losses in condition were similar in extent but more frequent than those experienced by hatchery trout in the Lower Dunk River.

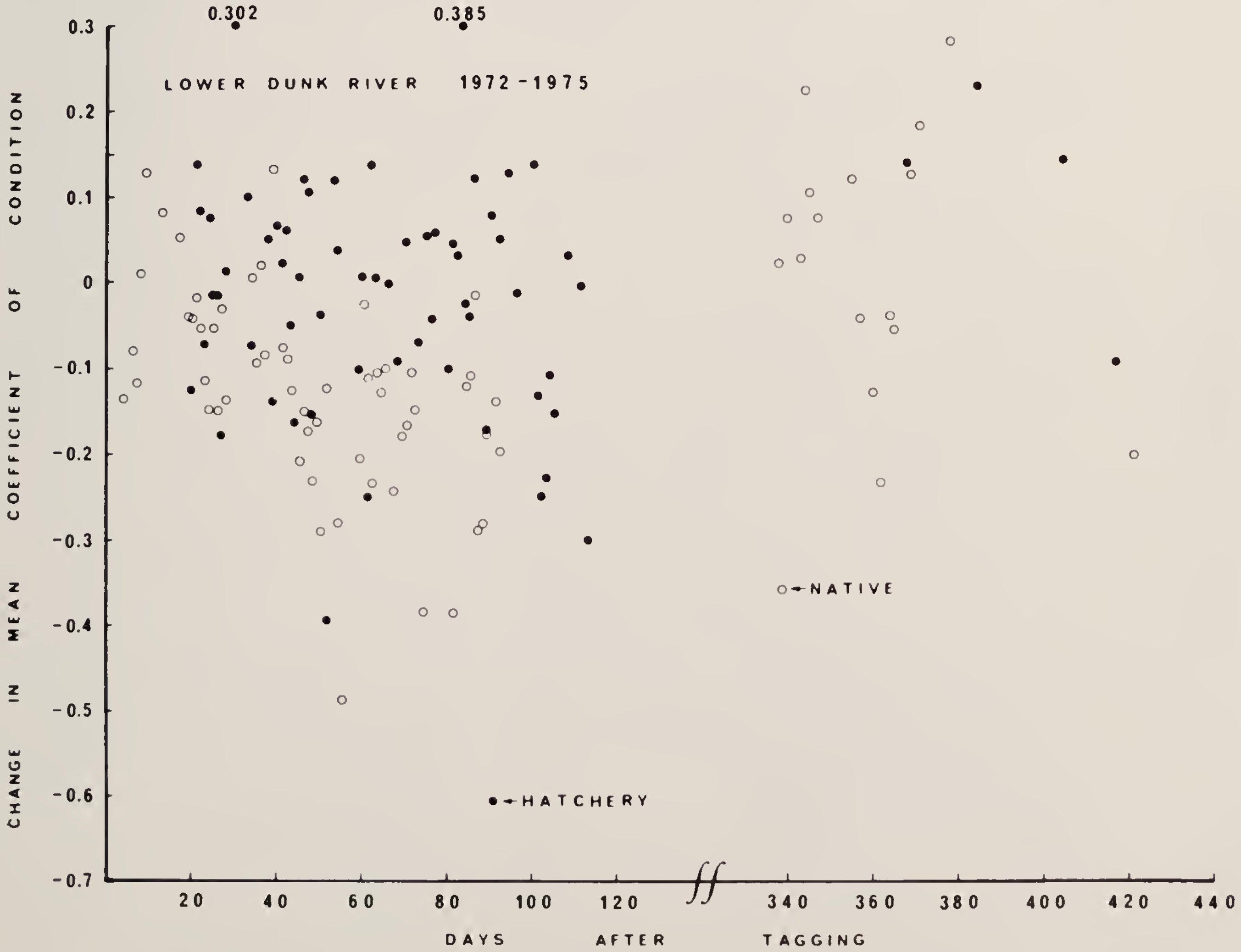

Fig 5. Changes in condition of brook trout following tagging in the Lower Dunk River.

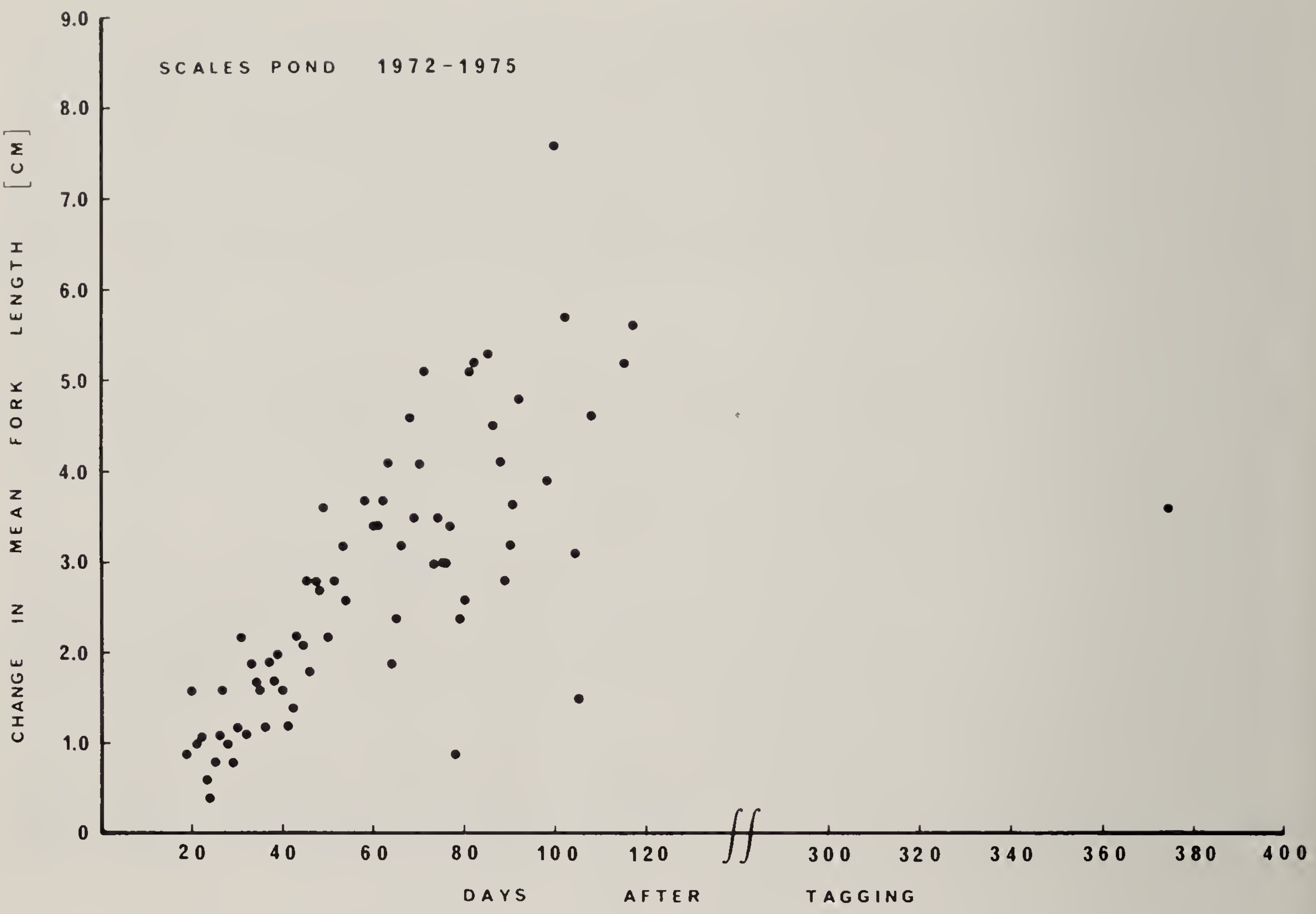

Fig 6. Changes in length of hatchery trout following tagging in Scales Pond.

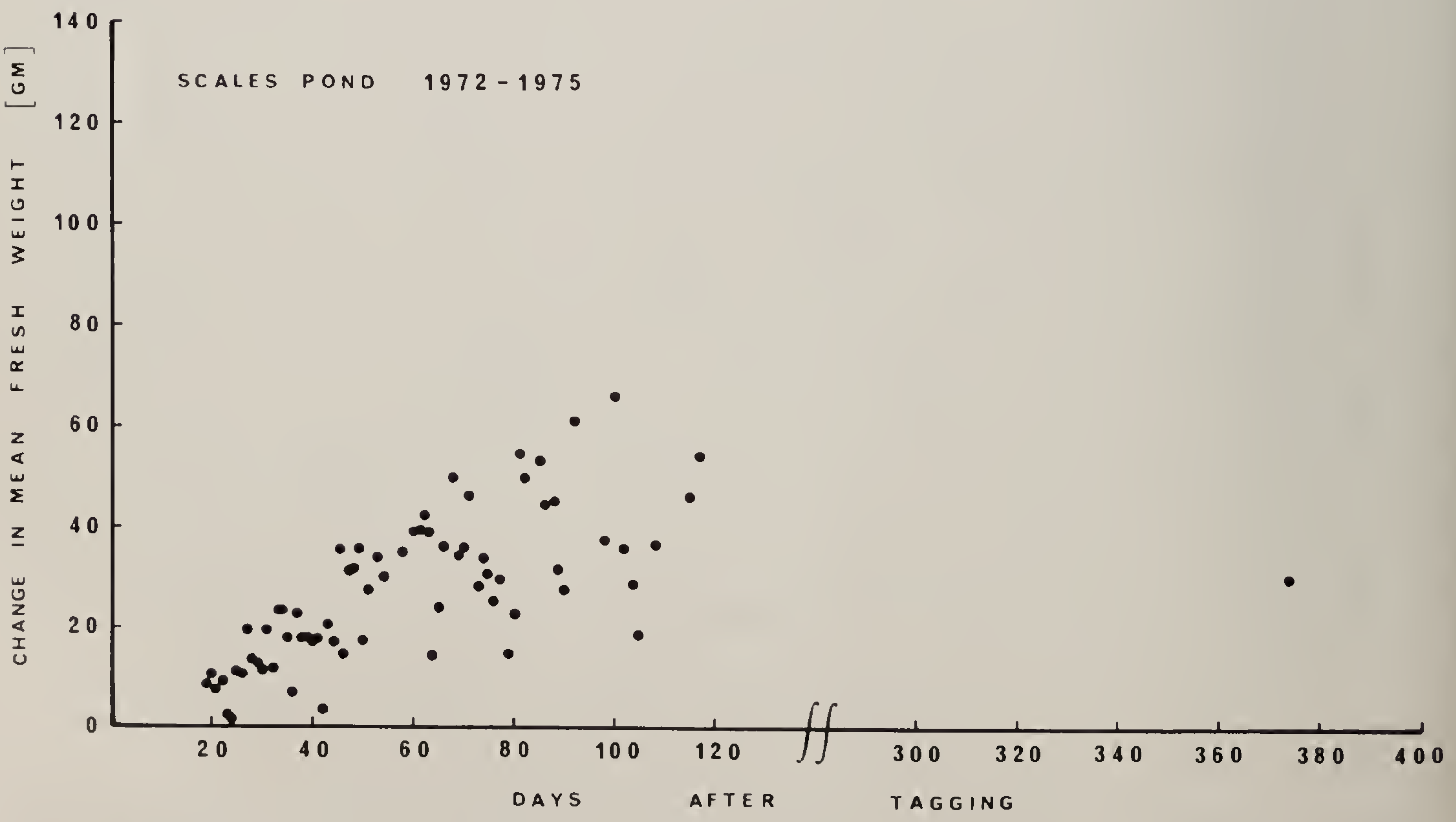

Fig 7. Changes in weight of hatchery trout following tagging in Scales Pond.

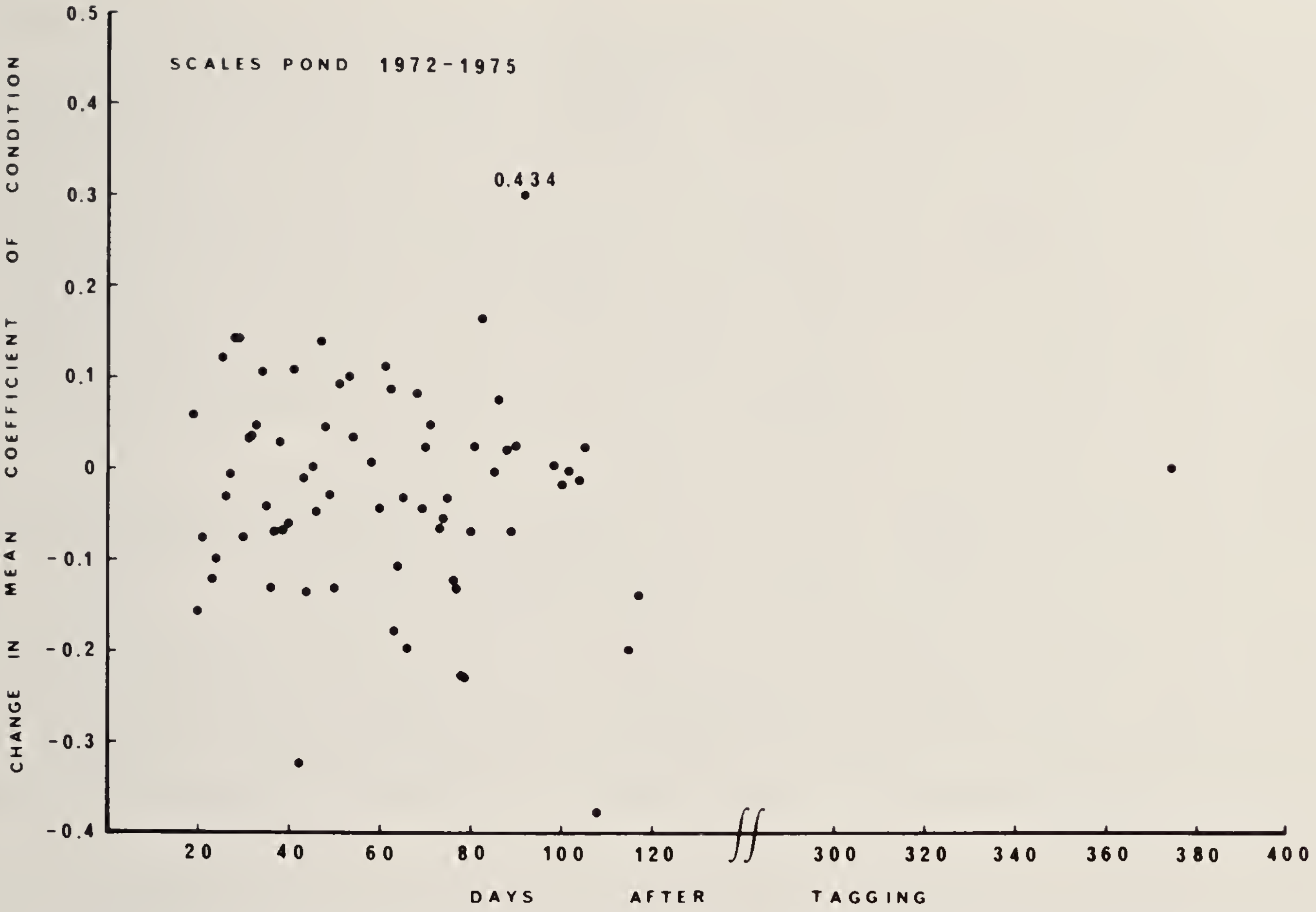

Fig 8. Changes in condition of hatchery trout following tagging in Scales Pond.

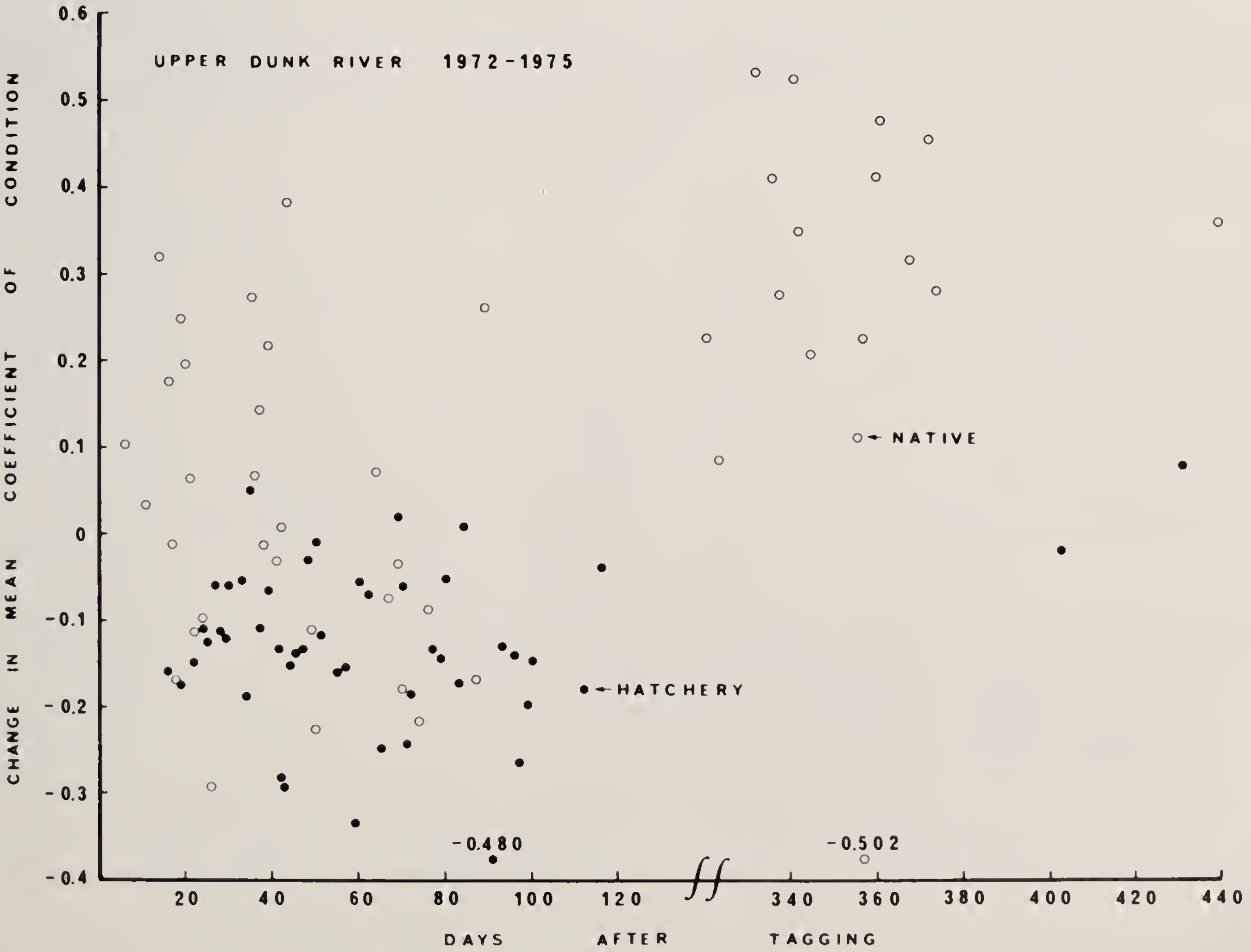

Fig 9. Changes in length of brook trout following tagging in the Upper Dunk River.

In the Upper Dunk River, 3974 tagged hatchery and 5622 tagged native brook trout were released; 207 and 1071, respectively, were later recaptured.

Changes in mean length and weight of tagged hatchery trout in the first 120 days after release were 3.5 to 4.5 cm (Fig 9) and 40 to 50 g. During the same period, tagged native brook trout gained only 2 to 3 cm and 10 to 15 g (Fig 10). Statistical treatment of the results indicated that weight and length gains for hatchery trout were significantly greater ($P<0.01$) than those for tagged native brook trout in that area.

Only 2 tagged hatchery and 18 tagged native brook trout were recaptured 320 to 440 days after release. The largest hatchery trout grew 7 cm and 118 g, while the tagged native trout grew an average of 6.8 cm and 62.6 g. These length and weight increments were not appreciably different for the two groups.

Almost all hatchery trout sampled from the Upper Dunk River declined in condition factor (Fig 11). Tagged native brook trout also showed losses in condition but the losses were not generally as great as those for hatchery trout.

In summary, weight and length increments for tagged hatchery and tagged native brook trout in the three different environments of the Dunk River system for the first 120 days after release suggest that hatchery trout grow significantly more in length and weight than native brook trout. Hatchery and native brook trout in the Lower Dunk River and Scales Pond also grew significantly better than those in the Upper Dunk River ($P<0.01$).

Better growth by hatchery and native brook trout in the Lower Dunk River during the first 120 days after tagging appears to be related in part to the food source. Hatchery and native trout in the Lower Dunk River fed extensively on eggs of smelt and gaspereau during spawning runs in May, June and July, and their stomachs were frequently distended with eggs. Other major foods included mayfly nymphs, caddisfly larvae and occasionally gastropods, adult smelts, and sticklebacks. Leeches, mayfly nymphs, dipterans, gastropods and sticklebacks formed the main food items in Scales Pond. Smelts and gaspereau were unable to pass the dam to spawn in the pond and therefore did not contribute to the food supply in that area. In the Upper Dunk River, trout fed primarily upon mayfly nymphs, caddisfly larvae, coleopterans

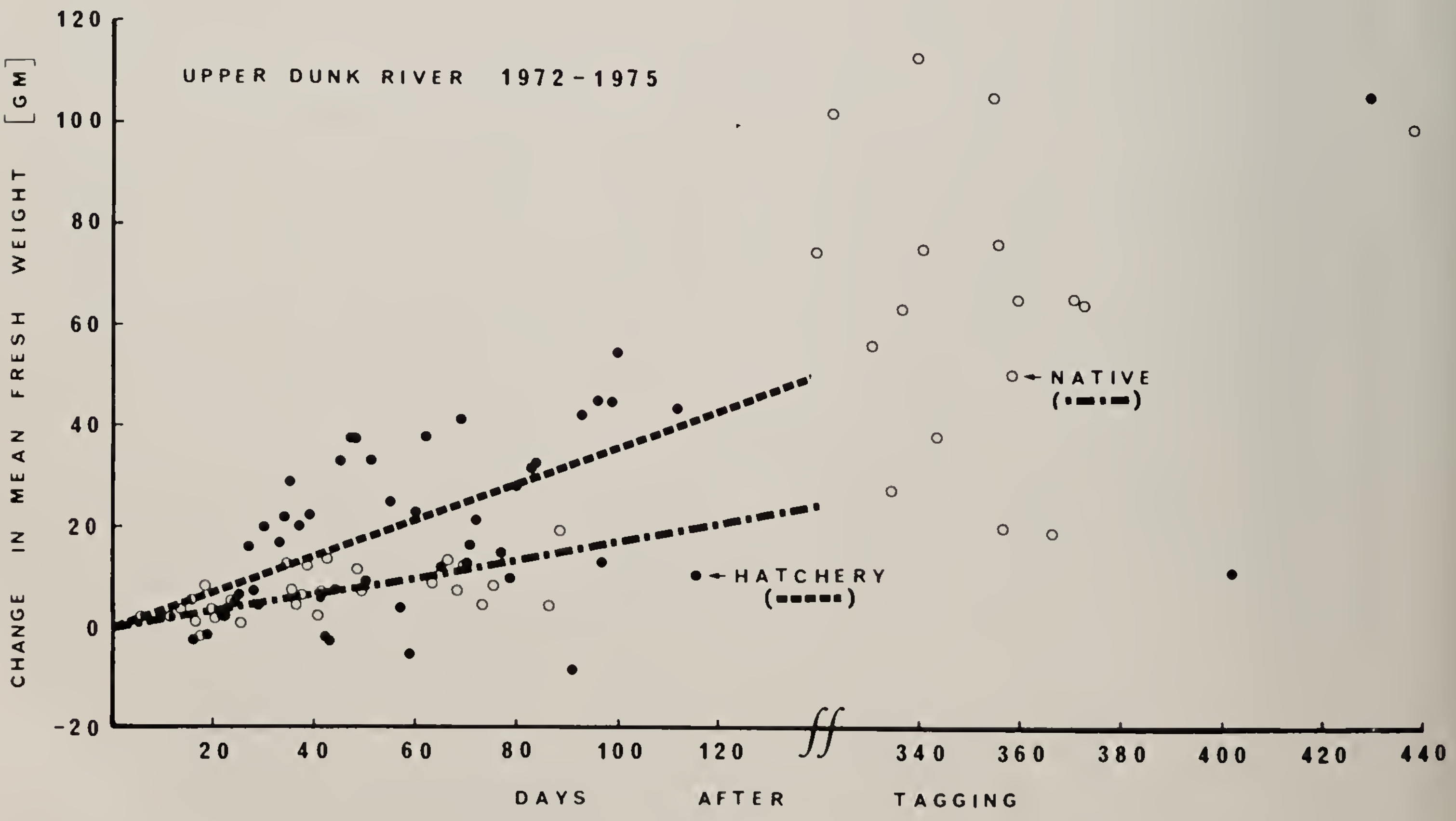

Fig 10. Changes in weight of brook trout following tagging in the Upper Dunk River.

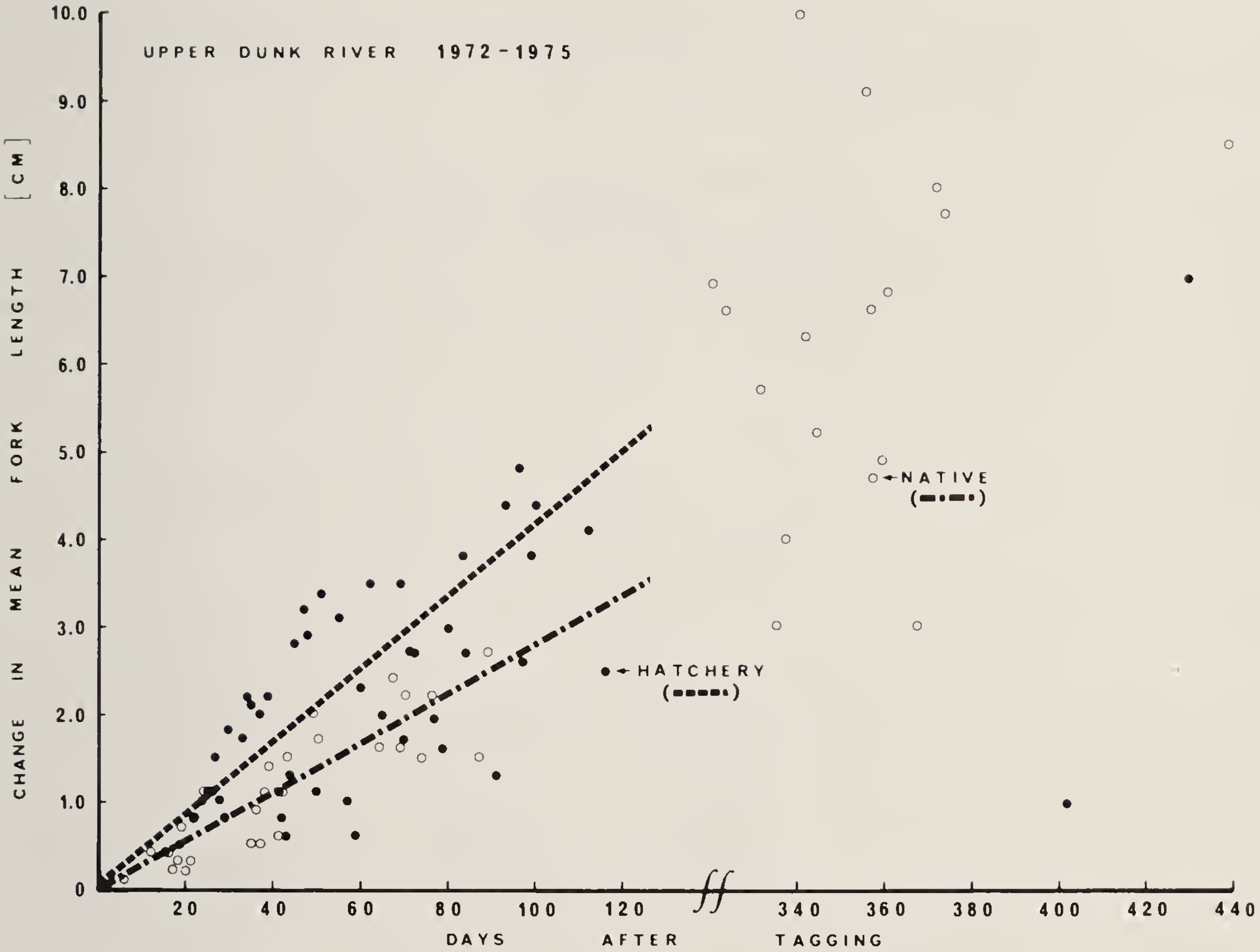

Fig 11. Changes in the condition of brook trout following tagging in the Upper Dunk River.

(mostly families Carabidae, Elmidae and Circuleonidae) and dipterans (mostly Chironomidae and Simuliidae). Generally, these food items were much smaller than those consumed by trout in the Lower Dunk River or Scales Pond. Furthermore, stomachs from trout in the upper region were seldom distended with food, unlike those in the lower river.

Poorer growth in the Upper Dunk River may also have been caused by overabundance of small trout. Site sampling in the Upper Dunk River indicated a high density of small native brook trout and rainbow trout of underyearlings, yearlings and 2-yr-olds (Table II). Such a combination of pressures may have adversely affected growth and compounded the effects created by food type.

The growth of tagged and untagged native trout was significantly lower than that for hatchery trout in the first 120 days after tagging in the lower and upper area. These differences in growth may have been caused by bolder feeding behavior and/or a faster growth by the hatchery strain.

The marginal difference in growth of tagged and untagged native trout in the Lower Dunk River suggests that jaw tags had little effect, in agreement with Shetter and Hazzard (1940), Smith (1957) and Youngs (1958). However, Smith (1957) found that growth of tagged brook trout in Prince Edward Island ponds became significantly lower after 248 days and this might have been also true in the Dunk River if trout had survived for a longer period of time.

Harvest of Hatchery Trout

The number of hatchery trout harvested by fishermen in 1972 was determined from jaw tags returned through the voluntary tag return program. The number of

Table II. Estimated average number of brook trout and rainbow trout in four sampling sites in the Lower Dunk River and three sampling sites in the Upper Dunk River during the summer months, 1972 and 1973.

Sampling period	Estimated average number of brook trout and rainbow trout/100 m^2	
	Lower Dunk River	Upper Dunk River
June	19	34
July	26	38
August	25	30
September	32	45
	25.5	36.7

Table III. Summary of the fate of hatchery trout planted in the Dunk River system in 1972.

Release site		Number released	Number caught[a]	% harvest[b]	Mean catch/h[c]
Lower Dunk River		989	116	11.7	0.2
Scales Pond	Lower	497	85	17.1	
	Middle	499	90	18.0	
	Upper	498	57	11.4	
	Total	1494	232	15.5	0.7
Upper Dunk River		998	164	16.4	1.1

[a] From voluntary fishing returns
[b] Calculated from number harvested/ total no. released x100
[c] Represents mean catch/hour for the fishing season.

hatchery trout caught based on the voluntary tag return program represents minimum harvest levels.

More jaw tags were returned by fishermen from hatchery trout in Scales Pond and the Upper Dunk River than in the Lower Dunk River (Table III). The high harvest in the pond as compared to the Lower Dunk River was associated with a better catch in the first month following release, when fishermen caught 8.3% of the hatchery trout released in the pond and only 3.8% of those in the Lower Dunk River. Most hatchery trout in the pond were caught within 1 km of the dam, whereas they were caught throughout the 7.6-km length of the Lower Dunk River.

The harvest of hatchery brook trout between 1973 and 1975 varied considerably between years and between areas (Table IV). The harvest of hatchery trout in the Lower Dunk River in 1974 was lower than the harvest in this area for the other years.

Table IV. Summary of the fate of hatchery trout after plantings in the Dunk river System during the period of May to September 3, 1973-75.

Year	Area	Number released	Number caught[a]	Estimated number caught[b]	% summer harvest[c]
1973	Lower Dunk River	970	38	173	17.8
	Scales Pond	1473	148	268	18.1
	Upper Dunk River	981	98	-	10.1
1974	Lower Dunk River	998	44	91	9.1
	Scales Pond	1498	174	295	16.7
	Upper Dunk River	999	-	-	-
1975	Lower Dunk River	998	129	302	30.3
	Scales Pond	1498	83	454	30.1
	Upper Dunk River	996	55	-	5.5

[a] Number counted in creel census, May 7-Sept. 3, except for Upper Dunk River where number caught is from voluntary fishing returns and creel census.
[b] Computed from creel census data, May 7-Sept. 3.
[c] Calculated using: estimated no. caught x 100/number released except for Upper Dunk River where actual catch was used in place of an estimate.

This was due probably to more frequent rain, cold weather, and very turbid water conditions (Fig 12). The apparently low harvest levels in the Upper Dunk River area in 1973 and 1975 may have been due to anglers not returning information about the capture of tagged trout or to less frequent fishing trips to that area. In 1972, 33 reports were received from anglers catching hatchery trout while in 1973 and 1975 there were only 14 and 17 reports, respectively.

Only 2 hatchery trout were reported caught by fishermen in 1973, 1 in 1974 and 2 in 1975 between September 4 and 30, the last day of the fishing season, suggesting that the harvest data for hatchery trout in Table V are reasonably close to the season levels.

The percentage harvest values for hatchery trout in this investigation are similar to those reported by Smith and Saunders (1968) for the Ellerslie system in Prince Edward Island and to those reported elsewhere (Alexander & Shetter 1969; Shetter & Hazzard 1940; Smith & Smith 1945; Trembley 1945).

Harvest of Tagged Native Brook Trout in the Lower Dunk River

In 1972, of 1239 native brook trout tagged in the Lower Dunk River area, 87 were recaptured in 1972 and 12 in 1973 while in 1973, of 637 brook trout, 64 were recaptured in 1973 and 13 in 1974.

Recoveries of Tagged Hatchery and Native Brook Trout

The estimated number of spring-released hatchery trout in the Lower Dunk River declined during the summer months (Table V), with few present after one year. While none was recovered after 1 year in samples taken for population estimates in July and August, 1974, a few were recovered in the creel censuses in May and June. Nine of the 989 hatchery trout released in 1972 were caught in 1973; 2 released in

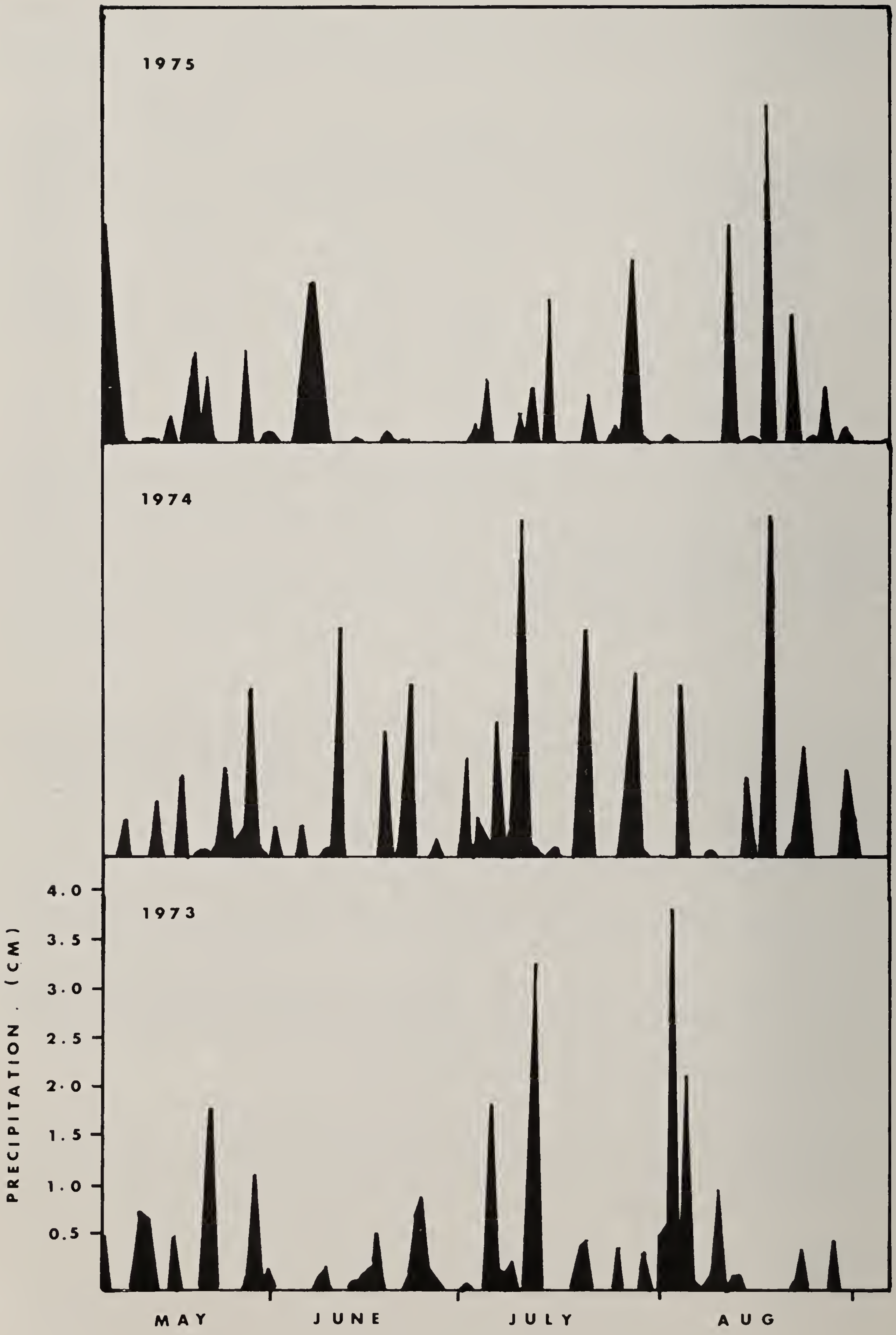

Fig 12. Summary of the daily summer precipitation levels for the Dunk River area between 1973 and 1975.

Table V. The estimated number and percent survival (parentheses) of hatchery trout released in the Lower Dunk River.

			Estimated number of hatchery trout in the Lower Dunk River		
Year released	Date released	Number released	Aug. 15th 1973	July 15th 1974	Aug. 15th 1974
1973	May 22	970	80(8.2)	0	0
1974	June 4	998	-	321 (32)	145 (14)

1973 were caught in 1974 and 6 released in 1974 were caught in 1975. During the entire study period, no hatchery trout was recaptured more than 1.5 years after release.

In Scales Pond, only 1 hatchery trout (released in June 1972) was recorded surviving more than 1 year (374 days).

There was a marked negative correlation between time of capture and size at release for hatchery trout in all areas (Fig 13). Larger trout at tagging were recaptured more frequently immediately following release and less frequently later in the season. Trout captured after more than 100 days were generally the smaller trout at tagging.

Based on catches of tagged native trout by anglers, an average of 1.5% of those tagged were caught in the next fishing season. This value is approximately twice that described for hatchery trout.

Poor recoveries of hatchery and native brook trout following release may have been caused by predation, competitive stress, movement, disease or excessive suspended sediment, of which the most probable are predation, competition and movement. Important predators were great blue herons *(Ardea herodias),* common mergansers *(Mergus merganser),* belted kingfishers *(Megaceryle alcyon)* and mink *(Mustela vison).* In May, June and July, as many as 10 to 15 herons/100 m of river were sighted in some areas, and following the release of hatchery trout in the Lower Dunk River, their number increased markedly (Fig 14). Also, observed throughout the summer were 4 pairs of kingfishers and 3 families of mink. During the winter, mergansers fished the open-water areas of the river and pond. Such predators may have taken hatchery trout more successfully than they did native trout. Smith (1955; 1968) found at Crecy Lake that implementing predator control improved survival and increased the percent harvest of trout. Butler (1975) reported that hatchery-reared trout use cover less, are more vulnerable to predation, and are more active and feed more than wild trout. Poor survival may be associated also with the fact that hatchery trout usually lack wildness. Stock selection by hatchery managers is usually for fast growth, resistance to disease, and adaptability to hatchery rearing. The qualities of wildness are important, for Mason et al. (1967), Flick (1971) and Flick and Webster (1976) have shown that greater longevity of hatchery-reared trout was consistently shown by wild and wild hybrid strains. Our findings support this, for survival to the next year, while low, appears to be twice as high for native trout populations.

Competitive stresses from native brook trout, rainbow trout, or Atlantic salmon may also have influenced the survival of hatchery trout during the summer. In the Lower Dunk River, populations for all 3 species combined ranged between 723 to 2660 trout per hectare. While the trout populations in Scales Pond are less certain, angler harvests indicated that native brook trout and rainbow trout together greatly

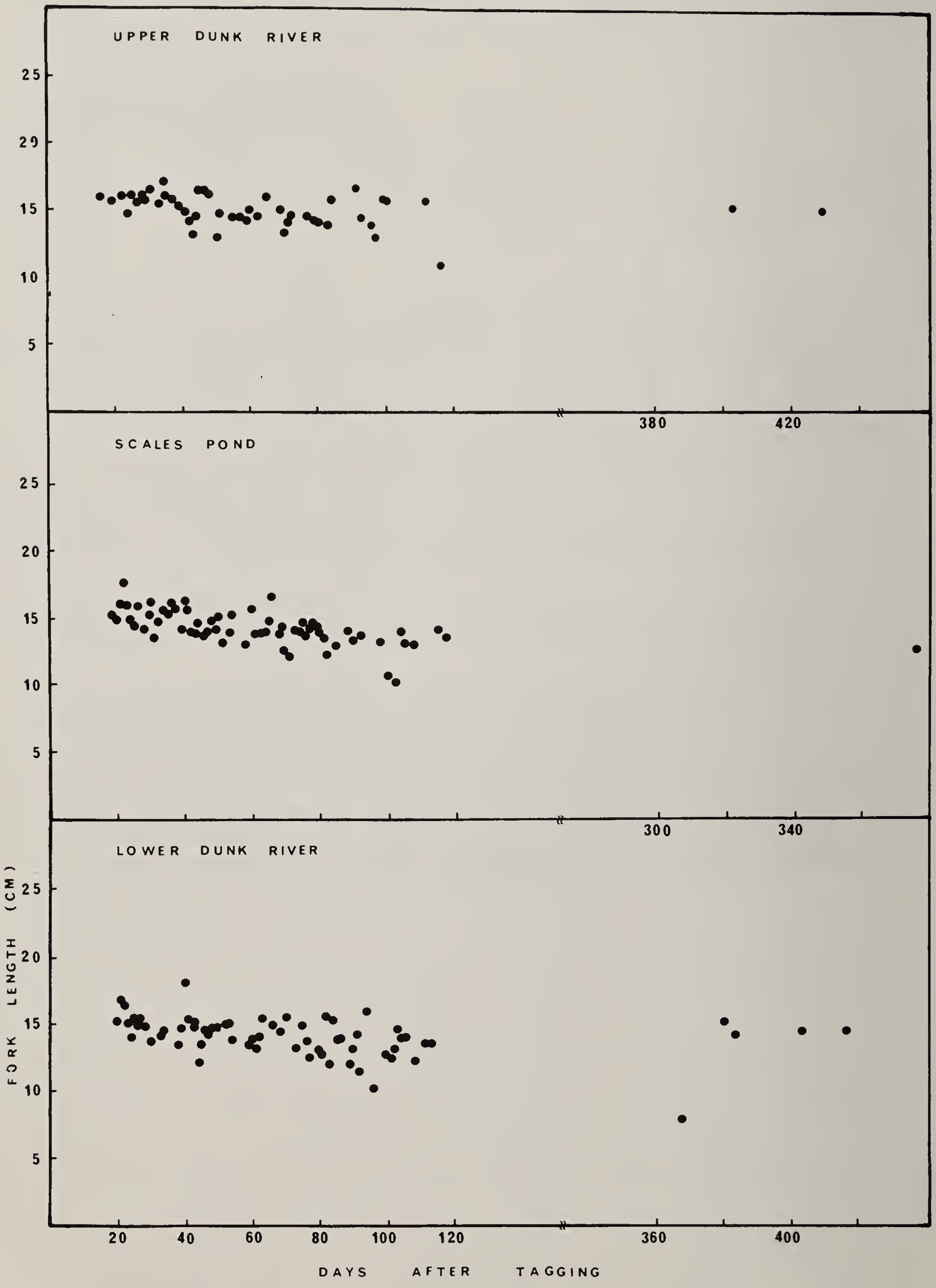

Fig 13. Summary of the mean fork lengths of hatchery trout at tagging as plotted against time of capture for the Lower Dunk River, Scales Pond, and the Upper Dunk River for the period 1972-1975.

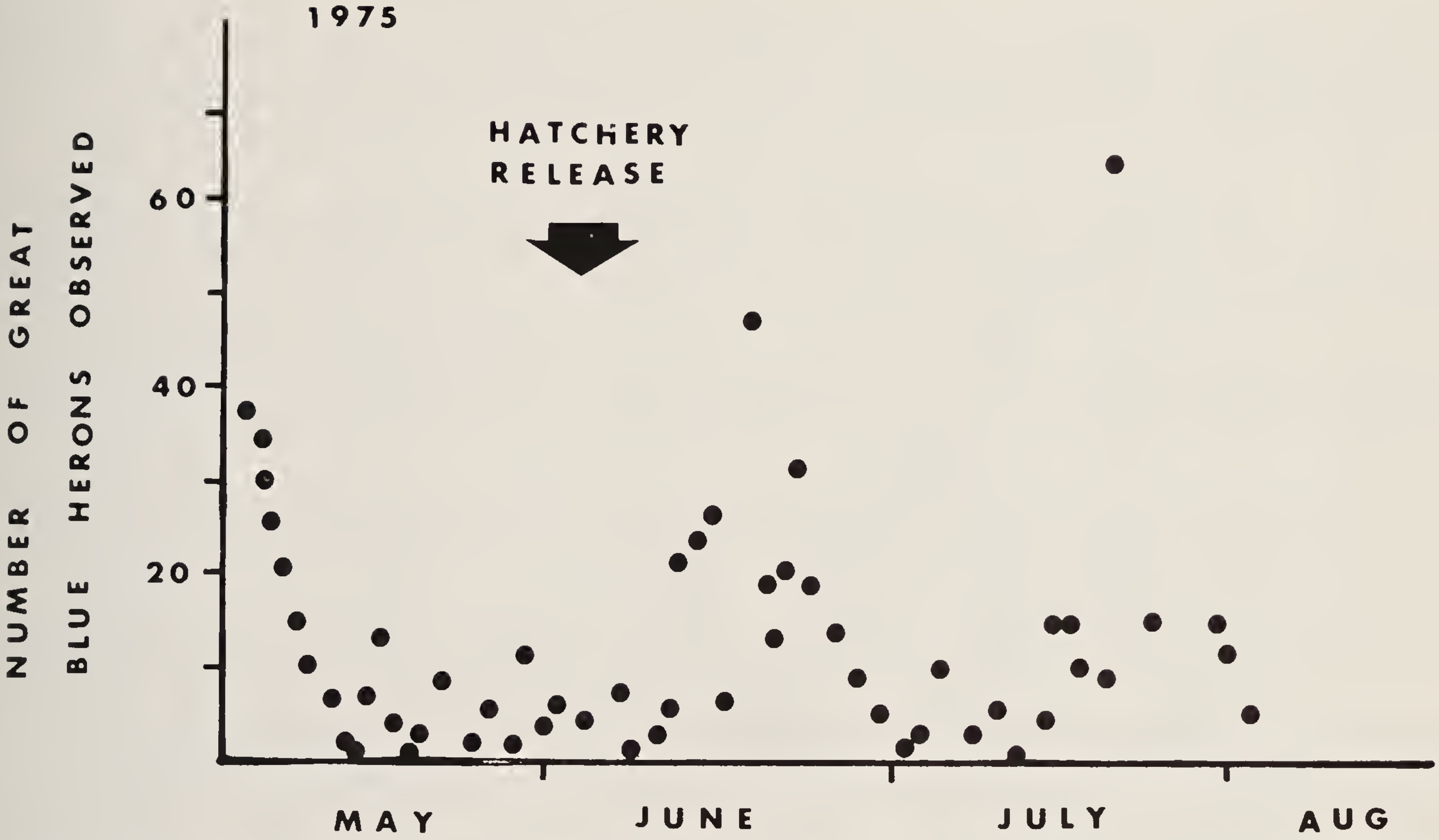

Fig 14. Summary of the number of great blue herons sighted daily in the Lower Dunk River during 1975.

exceeded 84 to 122 trout/ha. While competitive stress did not appear to affect the growth of those that survived, it may have greatly affected some of the weaker trout.

Movement of hatchery or tagged native brook trout out of the Dunk River system may have had a marked effect on recoveries. While hatchery trout planted in the Lower Dunk River moved generally upriver following release, at least 3 moved via the estuary to river systems adjacent to the Dunk systems and others were recaptured in the tributaries of the Dunk system. Of the hatchery trout planted in Scales Pond, 17% moved into the Lower Dunk River or its tributaries, and fewer than 1% moved into the Upper Dunk River. Of hatchery trout planted in the Upper Dunk River, at least 7% moved into Scales Pond or into the Lower Dunk River and its tributaries and a few moved upriver and were caught just below the impassable dam at Breadalbane. The extent to which all such movements influenced recoveries is not completely known.

Management Implications

Releasing hatchery-reared trout to the Dunk River system primarily increases angling success in the first summer after release, and mostly during the first month. The increased growth of hatchery trout did not appear to make them more capable of surviving to produce eggs and, in fact, it is unlikely they contributed in any measurable way to increasing trout production in the system.

Releasing hatchery-reared trout to the Dunk River system generally stimulated angling activity and harvest of native trout populations (Fig 15). With a long fishing season and a large daily creel limit (20 brook trout/day), overexploitation of trout populations can occur. According to fishermen, both the number and size of native brook trout in the Dunk River system have been declining in the last 10 years. Since the economic and recreational benefits of planting hatchery trout in the Dunk River system are limited, a careful review of present stocking policies should be conducted. Future plantings, if necessary, should be made with wild indigenous stocks that have sea-running characteristics. Stream enhancement programs designed to

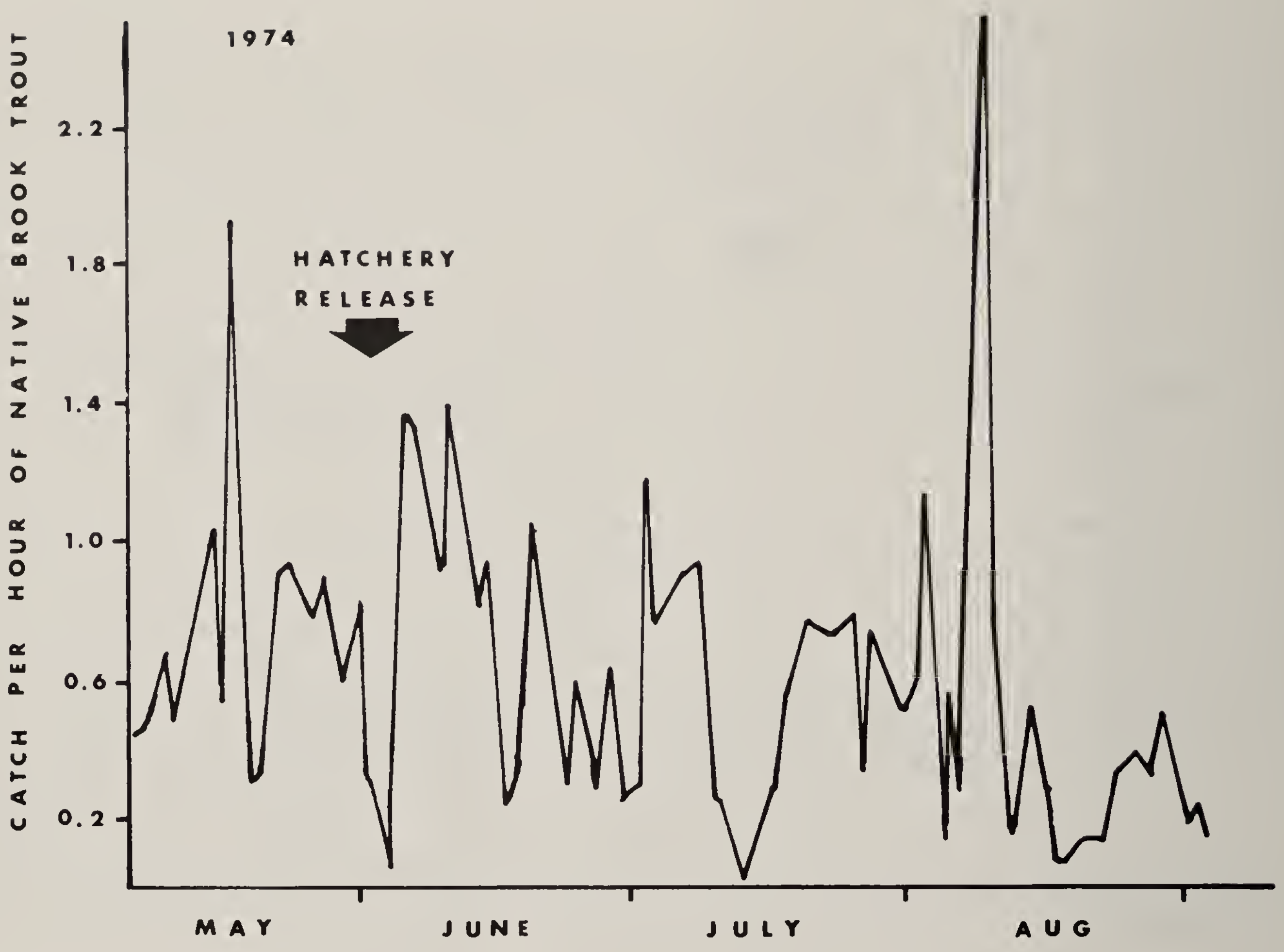

Fig 15. Summary of the daily catch per hour values for native brook trout prior to and following the release of hatchery brook trout in the Lower Dunk River in 1974.

improve food-producing rearing, and spawning habitats, combined with more protective regulations, are needed to ensure growth and development of wild trout populations.

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OBSERVATIONS ON THE FOODS OF BROOK TROUT (SALVELINUS FONTINALIS) AND RAINBOW TROUT (SALMO GAIRDNERI) IN THE DUNK RIVER SYSTEM, PRINCE EDWARD ISLAND

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Brook trout and rainbow trout in the coastal Lower Dunk River have considerable overlap in feeding habits from June to September and depend substantially upon eggs of anadromous smelts (Osmerus mordax) and gaspereau *(Alosa pseudoharengus)* during June and July. Lacking these foods, trout later feed primarily upon ephemeropteran nymphs, and dipteran and trichopteran larvae. Volumes of food consumed by both species were positively related to water temperature and food abundance, and in warmer water rainbow trout consumed more food than did brook trout. Brook trout and rainbow trout in a small inland stream environment of the same river system, while consuming invertebrates similar to those of trout in the coastal river environment, ate more terrestrial forms and had smaller food volumes. Significant differences in the growth of trout in the two environments were related to differences in diet and trout densities.

Introduction

High standing crops and rapid growth of young salmonids in streams and ponds of Prince Edward Island have been documented by White (1927; 1930), Saunders and Smith (1955; 1962) and Johnston and Cheverie (1980), and are related to the few predatory or rival freshwater fish species, high nutrient levels, and very abundant food.

Information on the food source for salmonids in Island waters is limited to some very general observations (White 1927; 1930; Smith 1936). None has described the abundance of the food source, the primary foods eaten or the seasonal patterns in dietary preferences. This study was undertaken to provide such information for brook trout and rainbow trout in a coastal river environment and an inland stream environment of the Dunk River system and to investigate the relationships between food and trout growth in those two environments.

Description of the Study Area

The Dunk River flows through agricultural lands in central Prince Edward Island (Fig 1). It is divided by dams into the Lower Dunk River, a coastal-river environment; Scales Pond, a freshwater-pond environment; and the Upper Dunk River, a small inland-stream environment. Detailed descriptions of the physical, chemical and biological features of the three environments have been published (Anon. 1974; Johnston 1974; Johnston & McKenna 1976; Johnston & Cheverie 1980; Staker 1976).

For this study, benthic invertebrates and trout were collected from the Lower Dunk River at site sampling areas 1 to 4, and from the Upper Dunk River at site sampling areas 5 to 7 (Fig 1).

Materials and Methods

Collection of Benthos

Prior to sampling, barrier nets were installed to enclose the study area. Bottom organisms were then collected from randomly selected 0.093-m^2 areas of the river

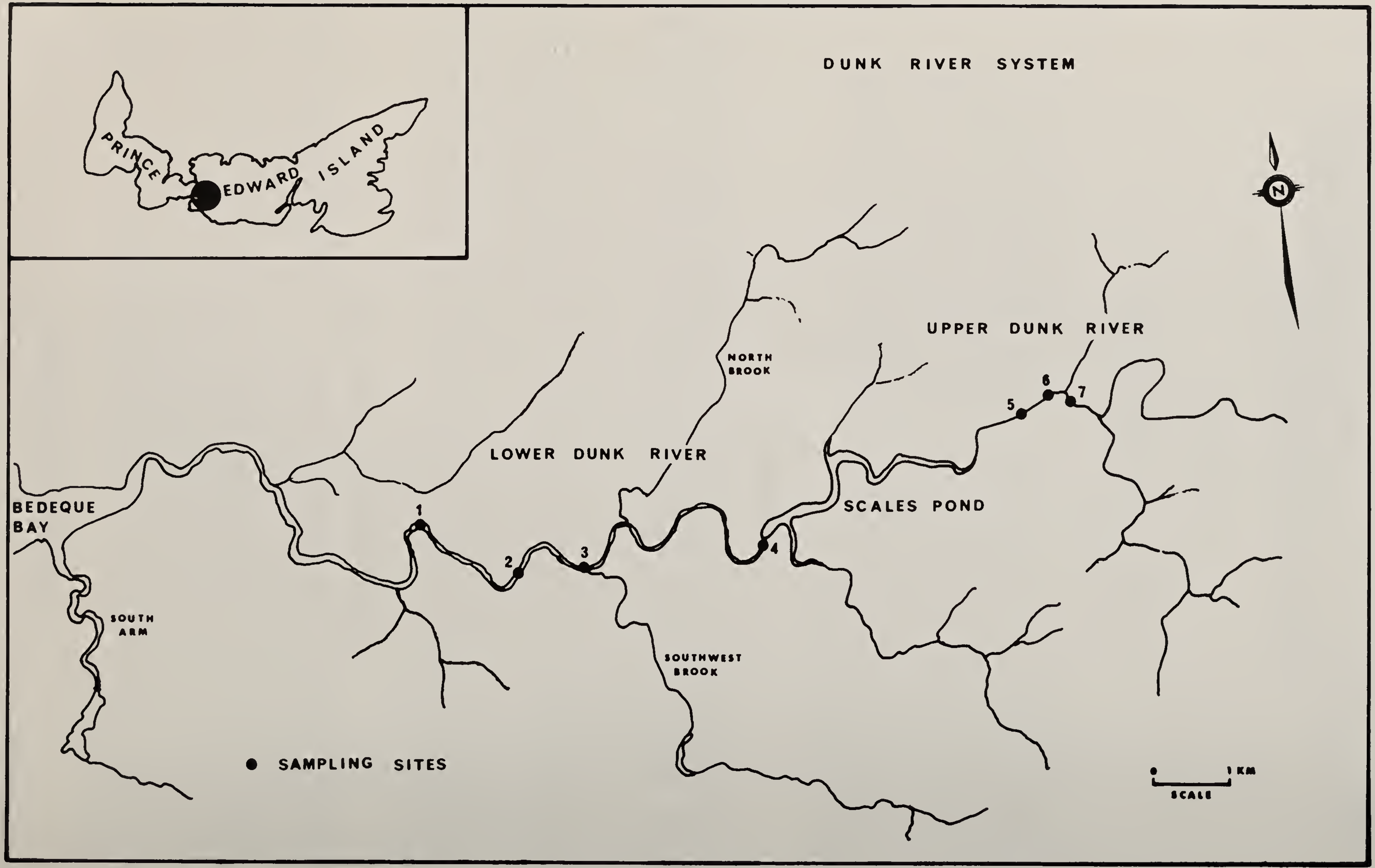

Fig 1. Location of the Dunk River study areas.

bottom using a Surber sampler. All stones and sediment in the sampling area were scrubbed by hand to wash benthic organisms into the collecting net. No attempt was made to prevent drift organisms from entering the collection net; however, collections were made as quickly as possible to prevent such contamination. Organisms collected from the net were preserved in a formalin-acetic acid-alcohol solution and later sorted, identified as to family and counted. Nymphs, larvae, pupae and adults were counted separately but later combined.

Collection of Trout and Stomach Samples

Brook trout and rainbow trout were collected from the areas between 0700 to 1000 using seining or electro-shocking equipment. Captured trout were quickly killed by a blow to the head and the entire gut and contents were removed and immediately fixed in 5-10% formalin. In the laboratory, each gut was carefully opened and the extent of stomach fullness assessed visually as: empty, trace, 1/4 full, 1/2 full, 3/4 full, full, distended. The gut contents were then removed and the food organisms separated, identified as to family and counted. The volume of each group of organisms was determined using volume-displacement techniques.

Because of their limited populations in the study areas, only small numbers of rainbow trout were retained for gut analysis.

Ivlev's (1961) elective index was computed using: $E_i = (C_i - P_i)/(P_i + C_i)$, where E_i is the Ivlev elective index for prey species i, P is the percentage composition of prey species i in the bottom sample and C_i is the percentage composition of prey species i in the stomach samples. Food preference is expressed by values from +1 to 0 while avoidance is expressed by values from 0 to -1.

Results

In June, a greater percentage of brook trout stomachs from the Lower Dunk River were full or distended with food than at other times of the study period or than brook trout stomachs from the Upper Dunk River (Table I). In the Lower Dunk River, the number of full stomachs declined and an increase in the number of empty stomachs occurred in late July. Empty or nearly empty stomachs in the Upper Dunk River did not increase in number until late August and September. The earlier increases in the number of empty stomachs in the Lower Dunk River may have been related to the presence of sea-running trout in the sample or to higher water temperatures.

Food Composition and Seasonal Trends

The data for the Lower Dunk River(Fig. 2)show that fish eggs, namely smelt and gaspereau eggs, play an important role in the diet of both brook trout and rainbow trout during June and July. Brook trout and rainbow trout ate 1.8 to 68.8% and 7.3 to 23.9% eggs (by volume), respectively, during this period. Ephemeropteran nymphs, dipteran larvae and trichopteran larvae were consumed by both species in smaller quantities. Most of the ephemeropterans belonged to the families Baetidae and Heptageniidae while the dipterans and trichopterans belonged in order of numerical importance to the families Chironomidae, Simuliidae, Tabanidae; Psychomiidae, Lepidostomatidae, Limnephilidae and Rhyacophilidae. In any sampling period, ephemeropterans never made up more than 25% of the total stomach volume in brook trout or 15% in rainbow trout; trichopterans never exceeded 10% in brook trout or 15% in rainbow trout. The number of dipteran larvae consumed by brook trout increased steadily during the summer and by August made up about 20% of the total stomach volume; values for rainbow trout were less than 10%.

Table I. Seasonal changes in the estimated stomach fullness of brook trout captured in the Lower and Upper Dunk River

	June 5— June 14		June 26— July 6		July 17— July 26		August 14— August 23		September 4— September 10	
Stomach fullness	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper
Empty	-	-	-	-	-	-	5.6	-	-	-
Trace	-	1.8[1]	13.6	3.7	17.8	6.7	9.3	17.5	2.0	20.0
1/4 Full	5.3	14.5	4.5	-	8.8	3.3	3.7	10.0	23.4	31.4
1/2 Full	12.2	20.2	11.4	14.9	17.8	13.3	27.8	27.5	21.6	14.3
3/4 Full	31.6	34.5	54.6	51.8	37.8	66.7	35.2	45.0	39.2	25.7
Full	45.6	29.0	15.9	29.6	17.8	10.0	18.5	-	11.8	8.6
Distended	5.3	-	-	-	-	-	-	-	2.0	-
Number sampled	57	55	59	74	58	30	94	40	51	35
Fork length range (cm)	10.0-26.3	7.2-18.3	8.7-26.0	8.8-17.5	6.8-22.5	6.6-17.3	7.0-20.5	6.6-17.1	8.1-21.5	6.7-13.6

[1] Percent of total sampled

In August and September, both trout species consumed large quantities of freshwater snails. The importance of snails in the diet remains obscure since samples from the hind gut were, except for erosion of the calcareous shells, mostly undigested. Trout may have eaten snails selectively to obtain algae on the shell or to obtain more calcium for the elaboration of gonadal tissue; alternatively they may have been feeding opportunistically, taking advantage of an abundant, less motile and more vulnerable organism. Elective index values (0.88-0.99) suggest that both brook and rainbow trout select this food.

In all the stomachs, 20 to 40% of the volume consisted of plant and other bottom debris such as small gravel, sand, and bits of wood. Most of the plant and bottom debris appeared to be from the cases of trichopteran larvae, however, some debris may have been ingested incidentally as trout foraged on the bottom or in the drift.

		JUNE 5 – JUNE 14	JUNE 24 – JULY 6	JULY 14 – JULY 26	AUG 1 – AUG 23	SEPT 4 – SEPT 10
STOMACHS SAMPLED	■	57	59	58	94	51
	○	21	8	11	16	
OLIGOCHAETA	■	14★	5	9	2	2
	○	14	12	27		
PLECOPTERA	■	14	3			
	○	38				
EPHEMEROPTERA	■	459	1652	179	765	2911
	○	2086	1088	182	1129	
TRICHOPTERA	■	89	107	115	36	40
	○	1176	187	200	64	
HEMIPTERA	■	10	20	19	37	11
	○	29	87	127	21	
COLEOPTERA	■	10	15	21	52	21
	○	29	300	82	36	
DIPTERA	■	182	451	786	1287	1652
	○	300	1525	836	1629	
HOMOPTERA	■	7	2			
	○		12			
LEPIDOPTERA	■	12	5	15	1	
	○	24				
HYMENOPTERA	■		27	41	19	6
	○	5	12	45		
GASTROPODA	■			9	97	238
	○	24		745	1321	
PELECYPODA	■					3
	○					
FISH EGGS	■	83263	6678	400		
	○	38181	5437			
FISH FRY	■	5	3			
	○					
DEBRIS	■	25☆	25	37	23	46
	○	24	38	40	20	

■ BROOK TROUT
○ RAINBOW TROUT
★ NUMBER REPRESENTS $\dfrac{\text{NUMBER OF FOOD ITEMS}}{\text{NUMBER OF STOMACHS SAMPLED}} \times 100$

☆ NUMBER REPRESENTS % TOTAL STOMACH VOLUME

Fig 2. Relative frequency of food items in the stomachs of brook trout and rainbow trout sampled from 4 sites in the Lower Dunk River.

More detailed seasonal analysis of bottom samples in Area 2 in the Lower Dunk River (Table II) indicated that benthic organisms became most numerous at the end of July (19,472 organisms/m^2) and declined to lower levels by mid- to late August (3,866 organisms/m^2). In all areas studied, rainbow trout consumed more food items per fish during periods of warmer temperatures than did brook trout. Rainbow trout also appeared to have preferred more surface or subsurface foods than did brook trout.

In the Upper Dunk River, brook trout consumed mostly ephemeropterans, dipterans and trichopterans (Fig. 3). Most of the families in each group were similar to those in the Lower Dunk River; however, unlike trout in the Lower Dunk River, trout

	JUNE 5 - JUNE 14	JUNE 26 - JULY 6	JULY 17 - JULY 26	AUG 14 - AUG 23	SEPT 4 - SEPT 10
STOMACHS SAMPLED	■ 55	■ 74	■ 30	■ 40	■ 35
OLIGOCHAETA	■ 149★	■ 32	■ 3	■ 2	■ 9
PLECOPTERA	■ 9	■ 4	■ 7	■ 5	■
EPHEMEROPTERA	■ 710	■ 740	■ 207	■ 40	■ 97
HEMIPTERA	■ 7	■ 31	■ 37	■ 10	■ 6
TRICHOPTERA	■ 227	■ 78	■ 97	■ 100	■ 31
COLEOPTERA	■ 171	■ 188	■ 47	■ 62	■ 60
DIPTERA	■ 609	■ 684	■ 840	■ 945	■ 837
HOMOPTERA	■ 7	■ 3	■	■ 2	■
LEPIDOPTERA	■	■ 8	■ 143	■ 5	■
HYMENOPTERA	■ 44	■ 54	■ 3	■ 5	■ 17
GASTROPODA	■ 5	■ 40	■	■ 25	■ 14
PELECYPODA	■ 14	■	■	■	■
NEMATODA	■ 53	■ 16	■ 43	■ 7	■ 51
FISH FRY	■	■ 12	■	■ 12	■ 6
DEBRIS	■ 28☆	■ 34	■ 38	■ 34	■ 38

■ BROOK TROUT

★ NUMBER REPRESENTS $\frac{\text{NUMBER OF FOOD ITEMS}}{\text{NUMBER OF STOMACHS SAMPLED}} \times 100$

☆ NUMBER REPRESENTS % TOTAL STOMACH VOLUME

Fig 3. Relative frequency of food items in the stomachs of brook trout sampled from 3 sites in the Upper Dunk River.

Table II. Summary of bottom and food organisms taken from sampling site 2 in the Lower Dunk River during June to August

Date	June 24			July 14		
	Brook trout	Rainbow trout	Bottom	Brook trout	Rainbow trout	Bottom
Number of samples	15	2		14	3	4
Fork length range (cm)	13.0-22.0	13.4-13.5		13.1-25.5	13.1-27.5	
Mean fork length (cm)	16.9	15.3		16.5	22.4	
Mean fresh weight (g)	70.1	73.9		79.1	177.1	
Total number of food organisms	496	26		54	17	3286
Number of organisms consumed/fish	33.1	13.0		3.8	5.7	
Number of bottom organisms/m^2						8847
Number of fish with empty guts	0	0		1	1	

Date	July 30			August 18		
	Brook trout	Rainbow trout	Bottom	Brook trout	Rainbow trout	Bottom
Number of samples	17	4	4	24	11	2
Fork length range (cm)	12.1-44.7	14.5 43.0		8.7-32.2	7.5-30.0	
Mean fork length (cm)	20.7	26.5		15.3	17.3	
Mean fresh weight (g)	86.9	404.1		72.8	119.4	
Total number of food organisms	64	195	7235	799	400	718
Number of organisms consumed/fish	3.8	48.8		33.39	36.4	
Number of bottom organisms/m^2			19480			3787
Number of fish with empty guts	1	2		0	0	

in the Upper Dunk River consumed a much larger percentage of terrestrial invertebrates. Many of the terrestrial invertebrates such as ants and a variety of beetles probably fell from the dense alder overhang along the river banks to become part of the drift. Because of the narrowness of the Upper Dunk River (7.9-12.0 m), drift organisms were more readily available to trout than in the Lower Dunk River (width 9.6-17.0 m).

The stomach contents of the few rainbow trout from the Upper Dunk River differed little from those of brook trout. However, in both areas, rainbow trout had a greater preference for adult food organisms than did brook trout (Table III), and brook trout preferred nymphs more than did rainbow trout. Regardless of area, both species preferred nymphs to larvae, and fish predation and cannibalism contributed little to the diet of either species, reflecting the abundance of invertebrates in the Dunk River system.

Discussion

These results clearly demonstrate that anadromous fish species spawning in the spring and early summer, supply important foods for both salmonid species in the coastal river environment. Without this food source, growth of brook trout is

Table III. Number, percent occurrence of different insect stages observed in stomach and bottom samples, and elective index (E). Samples were taken from 4 sampling sites in the Lower Dunk River and 3 sampling sites in the Upper Dunk River between June 18 and July 30

	Lower Dunk River				
	Brook trout	E	Rainbow trout	E	Bottom samples
Larva	170[1] (16.3)[2]	-0.64	285 (47.1)	-0.22	7383 (74.1)
Nymph	830 (79.5)	0.63	290 (47.9)	0.45	1794 (18.0)
Pupa	22 (2.1)	-0.52	4 (0.7)	-0.81	665 (6.7)
Adult	22 (2.1)	0.27	26 (4.3)	0.56	116 (1.2)
Total	1044		605		9958

	Upper Dunk River				
	Brook trout	E	Rainbow trout	E	Bottom samples
Larva	65 (16.6)	-0.68	3 (7.9)	-0.83	2064 (86.5)
Nymph	193 (49.3)	0.61	15 (39.5)	0.54	281 (11.8)
Pupa	19 (4.8)	0.65	-		24 (1.0)
Adult	115 (29.3)	0.95	20 (52.6)	0.97	17 (0.7)
Total	392		38		2386

[1] Number of organisms
[2] Percent of total number of all stages

Table IV. Seasonal changes in the average volume of food per trout stomach. Debris was not included in volume determinations

	Lower Dunk River				Upper Dunk River	
Sampling period	Brook trout	N[1]	Rainbow trout	N	Brook trout	N
June 5—June 14	1.99[2] (15.1)[3]	57	1.41 (16.5)	21	0.31 (11.2)	55
June 24—July 6	0.49 (15.8)	59	0.65 (14.8)	8	0.37 (12.6)	74
July 14—July 26	0.15 (13.8)	58	0.32 (16.8)	11	0.19 (11.5)	30
Aug. 1—Aug. 23	0.20 (11.8)	94	0.40 (16.2)	16	0.12 (10.2)	40
Sept. 4—Sept. 10	0.55 (13.2)	51	-		0.06 (10.0)	35

[1] N = Sample size
[2] Average volume (ml) of food per trout stomach
[3] Mean fork length (cm)

significantly reduced (Johnston & Cheverie 1980). In view of the extensive overlap in foods consumed by brook trout and rainbow trout, growth of rainbow trout was probably influenced in a similar way, but insufficient growth data have been collected to verify this.

While brook trout and rainbow trout in the Upper Dunk River did not benefit from the organic influx from the marine environment, they did have the more available and probably more abundant terrestrial food source of the surrounding agricultural region. Such terrestrial foods appear to be more important in the diet of rainbow trout than of brook trout and this may be related to the more active surface or subsurface feeding behavior of the former species.

The great diversity of food organisms in the diet of both brook trout and rainbow trout suggests that they are opportunistic feeders. While most foods consumed were highly motile forms, others such as snails, fish eggs and pupae were not. It is difficult to know with certainty whether these inactive forms were in the drift or on the bottom, but probably foraging occurred both from the bottom and from the drift.

Seasonal changes in population density of benthic organisms and volume of foods in the stomach of both trout species were evident. More was eaten by brook trout when water temperatures were cooler and food abundant (Table IV). These findings are similar to studies elsewhere (Gibson & Galbraith 1975; Logan 1963). In rainbow trout, when water temperatures were warm, the food volumes were almost twice those of brook trout.

In the Upper Dunk River food volumes were much lower; this may be related to the food source, competition, or to the size of stomachs. While only minor differences were observed in the number of bottom organisms/m^2 for the Lower and Upper Dunk River areas between late June and early July, more obvious differences were apparent in trout densities (Johnston & Cheverie 1980) and in mean fork lengths.

Since growth and production of salmonids and benthic food organisms in coastal rivers of Prince Edward Island appear greatly enhanced by spawning smelts and gaspereau, fisheries managers should ensure in the future that such migratory anadromous species have unimpeded movement throughout an entire river system.

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ANGLER HARVEST OF NATIVE BROOK TROUT (SALVELINUS FONTINALIS) AND RAINBOW TROUT (SALMO GAIRDNERI) POPULATIONS IN THE DUNK RIVER SYSTEM, PRINCE EDWARD ISLAND

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Angler harvest of native brook trout and rainbow trout populations were investigated in the Dunk River system, P.E.I. from 1972 to 1975. Of the fishermen interviewed, 89.2% were residents of P.E.I., 91.3% of these were males, and most lived within 10.0 to 20.0 km of the river. During the summer months, 50.9 to 143.2 h ha^{-1} were expended fishing in the Lower Dunk River with more during late spring than late summer. Fishing pressure on Scales Pond was much lower. Residents angling in the coastal river environment caught between 164 and 245 brook trout ha^{-1} (18.3-23.6 kg ha^{-1}) and 30 to 36 rainbow trout ha^{-1} (6.0-6.7 kg ha^{-1}). Non-residents caught only 11 to 19 brook trout ha^{-1} (1.1-2.1 kg ha^{-1}) and 3 to 5 rainbow trout ha^{-1} (0.3-0.9 kg ha^{-1}). Estimates of harvest were much lower for Scales Pond, 15 to 106 brook trout ha^{-1} (1.1-4.0 kg ha^{-1}) and 2 to 7 rainbow trout ha^{-1} (0.5-1.3 kg ha^{-1}) for residents, and 1 to 4 brook trout ha^{-1} (0.1-0.3 kg ha^{-1}) and 0.2 to 0.7 rainbow trout ha^{-1} (0.04-0.2 kg ha^{-1}) for non-residents. Population estimates for 2+ and older trout ranged between 236 and 570 brook trout ha^{-1} and 78 to 118 rainbow trout ha^{-1}. Estimates of total biomass for 0+ and older trout varied from 28.1 to 86.0 kg ha^{-1} for brook trout and 6.0 to 17.7 kg ha^{-1} for rainbow trout for the 2 yrs. Minimum exploitation rates of the precensused brook trout population in May in the Lower Dunk River varied from 0.26 to 0.44 for brook trout and from 0.33 to 0.47 for rainbow trout during 2 yrs of the study.

Introduction

Recreational fishing in Prince Edward Island has been steadily increasing during the last 25 years. Acres Research and Planning Limited (1967) reported that the number of angling licenses sold between 1950 and 1954 increased by 1960 to 1964 by 50% for resident and 58% for non-resident anglers. A more recent study by Thomson (1976) showed that the number of licenses issued between 1966 and 1974 increased a further 29%. With a growing human population in urban centers and a growing tourist industry, angling pressure will continue to increase in the future and will make accessible trout populations more susceptible to overfishing.

Information concerning the characteristics of trout populations and of angler harvest in ponds, rivers and estuaries of Prince Edward Island is limited to the reports by Smith (1947; 1951; 1963), Smith and Saunders (1968), Saunders and Smith (1955; 1964), Thompson (1976) and, most recently, an anonymous survey (Anon. 1978).

The objectives of this 3-year study were to evaluate the effect of angling and other factors on the sport fishery in two regions of the Dunk River system and to establish base-line data so that any future changes in the fishery could be recognized and evaluated.

Description of the Study Area

The Dunk River system flows through agricultural lands of eastern Prince and western Queens Counties and discharges into Bedeque Bay (Fig I). The system is divided by dams into the coastal Lower Dunk River, the freshwater Scales Pond and the small inland Upper Dunk River. The Lower Dunk River and Scales Pond are

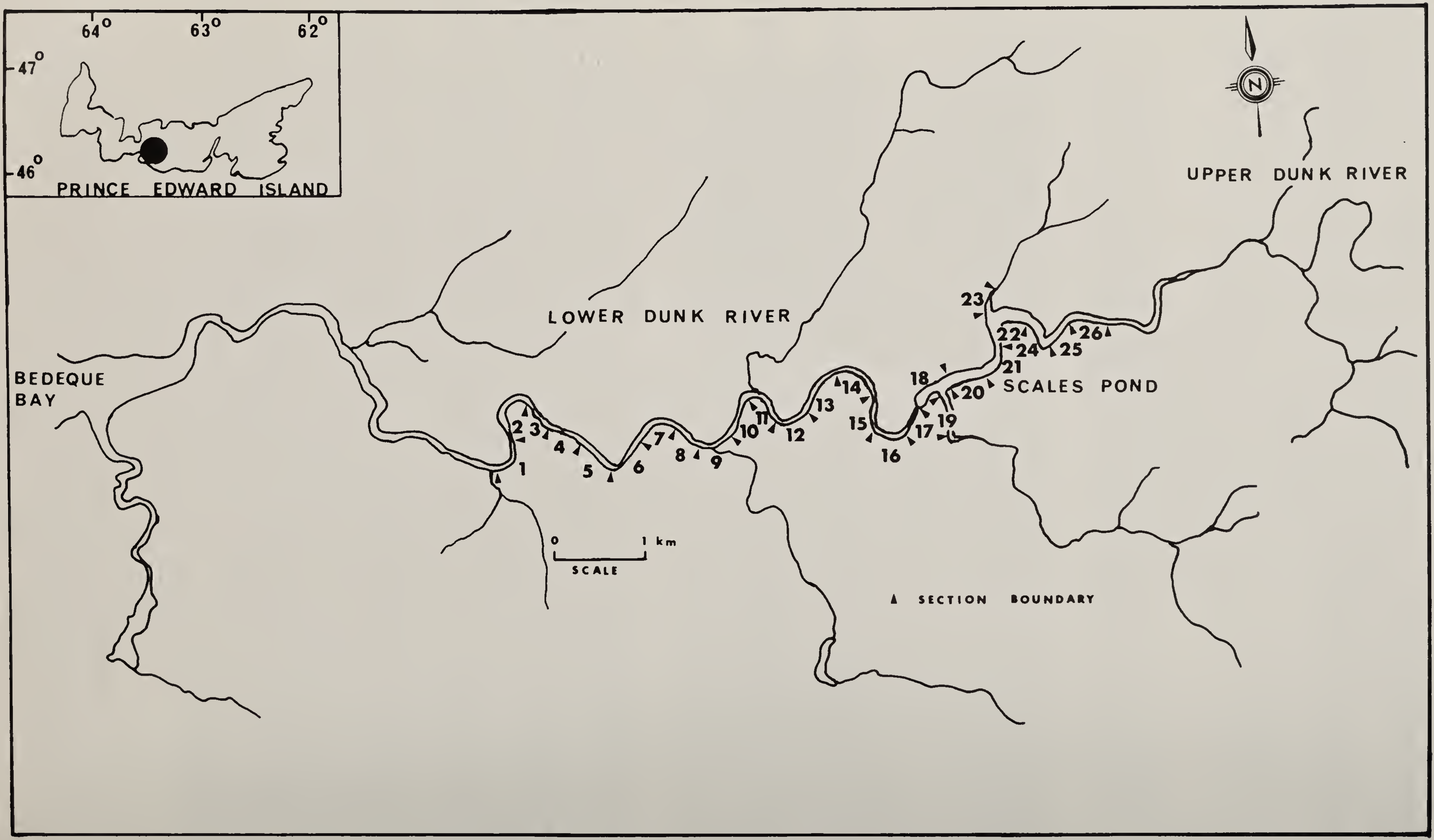

Fig 1. Location of the study area and sections used in defining the catch by area for Lower Dunk River and Scales Pond.

separated by an impassable dam, making it possible to describe separately the characteristics of the sportfishery for each area.

The physical, chemical and biological features of the Lower Dunk River and Scales Pond have been described already in earlier publications (Anon. 1975, Johnston 1974, Johnston & McKenna 1976, Johnston & Cheverie 1980; Staker 1976).

Aspects of the Dunk River Sportfishery

The Dunk River sportfishery is based upon the brook trout *(Salvelinus fontinalis)*and the rainbow trout *(Salmo gairdneri).* Atlantic salmon in the Lower Dunk River contribute little to the summer sportfishery, because adult fish are rare and arrive only in late fall. The dominant sportfish is the indigenous sea-running speckled brook trout. These are much sought after by local and visiting anglers, who have caught fish larger than 2 kg during spring or fall runs.

Since 1913, sea trout populations have been supplemented annually with hatchery-reared brook trout. Most plantings prior to 1960 were with fry hatched from eggs collected locally, but plantings after that date were mostly with yearlings, cultured from domesticated strains from Nova Scotia or New Brunswick (Table I). The contribution of domesticated hatchery-reared brook trout to the Dunk River sportfishery has been assessed in another report by Johnston and Cheverie (1980).

Unlike the indigenous brook trout, rainbow trout were first introduced to the Dunk River System in 1941 and were stocked sporadically until 1964 (Table II). Rainbow trout have become naturalized and now maintain their numbers through reproduction. In recent years, some have been caught weighing more than 3.6 kg. Stocks in the Lower Dunk River run to the sea and return to the river throughout the summer and fall to spawn in early winter and spring. Because of the impassable dam at Scales Pond, brook and rainbow trout cannot move into Scales Pond from the Lower Dunk River.

The fishing season for both species in Prince Edward Island begins on April 15 and terminates on September 30. The daily creel limit is 20 brook trout and 5 rainbow trout per day with no annual limit.

Methods

Stratified Creel Census

The angler harvest was determined in 1973-75 through a stratified creel census conducted on the Lower Dunk River and Scales Pond between May 7 and September 3. The fishing season from April 15 to May 6 and from September 4 to 30 was not censused. Except for opening day and the first few weekends, fishing pressure is less during the first 22 days and the last 27 days of the fishing season than during the rest of the season. The census and harvest-estimate methods have been described before (Johnston & Cheverie 1980).

Population Estimates in the Lower Dunk River

In 1973 and 1974, brook trout and rainbow trout populations in the Lower Dunk River were estimated by sampling randomly selected areas of the river with electrofishing equipment, according to the methods described already by Johnston and Cheverie (1980).

Weight Determinations

Throughout the study period, accurate weight and length measurements for native brook trout and rainbow trout were taken monthly during site sampling. These data were used to calculate weights from lengths of fish recorded in the creel census and population study, using the relationship $W = aL^b$ where in any month

Table I. Stocking history for the Dunk River system, 1960 to 1975 inclusive

		Lower Dunk River		Scales Pond		Upper Dunk River		Wrights Pond	
Year	Release Period	Brook Trout	Rainbow Trout	Brook Trout	Rainbow Trout	Brook Trout	Rainbow	Brook Trout	Rainbow Trout
1960	Spring	4,000(2)*	-	12,000(2)	-	-	-	-	-
	Fall	-	-	5,000(3)	-	-	-	-	-
1961	Spring	-	-	-	-	-	-	-	-
	Fall	4,800(4)	-	8,000(3,4)	7,800(3)	-	-	-	-
1962	Spring	-	-	-	-	-	-	-	-
	Fall	6,000(4)	-	6,000(4)	-	-	-	3,000(3)	-
1963	Spring	-	-	-	-	-	-	-	-
	Fall	4,200(3)	6,270(3)	4,200(4)	6,270(3)	-	-	-	-
1964	Spring	-	-	-	-	-	-	-	-
	Fall	4,500(4)	5,000(3)	4,500(4)	5,000(3)	-	-	-	-
1965	Spring	-	-	-	-	-	-	-	-
	Fall	3,240(4)	-	4,050(4)	-	-	-	2,430(4)	-
1966	Spring		-	-	-	-	-	-	-
	Fall	1,680(sf)	-	-	-	-	-	2,500(3)	-
1967	Spring	1,700(sf)	-	-	-	-	-	-	-
	Fall	1,350(3)	-	1,360(3)	-	-	-	-	-
1968	Spring	-	-	-	-	-	-	-	-
	Fall	1,000(4)	-	5,000(4) 840(5)	-	5,000(4)	-	2,000(4)	-
1969	Spring	-	-	-	-	-	-	-	-
	Fall	-	-	-	-	-	-	-	-
1970	Spring	2,000(sf)	-	2,500(sf)	-	-	-	-	-
	Fall	-	-	-	-	-	-	-	-
1971	Spring	-	-	-	-	-	-	-	-
	Fall	5,500(4)	-	7,000(4) 4,000(sf)	-	-	-	2,500(4)	-
1972	Spring	989(sf)	-	1,494(sf)	-	998(sf)	-	3,000(4)	-
	Fall	-	-	-	-	-	-	-	-
1973	Spring	970(sf)	-	1,473(sf)	-	981(sf)	-	1,000(sf)	-
	Fall	-	-	-	-	-	-	-	-
1974	Spring	998(sf)	-	1,498(sf)	-	999(sf)	-	-	-
	Fall	-	-	-	-	-	-	-	-
1975	Spring	998(sf)	-	1,498(sf)	-	996(sf)	-	-	-
	Fall	-	-	-	-	-	-	-	-

*The numbers or letters in parentheses represent the stage of trout development: 1— 8 weeks after systematic feeding begins 2—14 weeks after systematic feeding begins 3—20 weeks after systematic feeding begins 4—26 weeks after systematic feeding begins 5—26 weeks—1 year after systematic feeding begins sf—yearling the coefficients a and b were determined from fish measured. Weights for trout caught by fishermen during May were computed from a and b values derived from the site sampling in June.

Results

While the number of resident and non-resident angling licences purchased in Prince Edward Island during the last 20 years has been steadily rising, the number of anglers interviewed on the Dunk River System did not increase markedly during the study period. During the study, 3,758 resident and 453 non-resident fishermen were interviewed on the Lower Dunk River and 1,381 resident and 172 non-resident anglers were interviewed on Scales Pond. Of those interviewed, 89.2% were residents, of which 91.3% were males, and 11.4% of them less than 16 years of age (compared with only 1.2% of the resident female group). Similar findings were documented for non-resident male and female anglers, respectively.

Angler Origin

In all years, over 75% of the angling trips were made by fishermen who lived within 10.1 to 20.0 km of the river (Table III). Only a small percentage of the trips (5.0-12.5%) were made by fishermen living along the river or living more than 20 km away.

Most of the non-resident angler trips (72.3-83.9%) were made by Canadians who were more frequently from Ontario, Nova Scotia, New Brunswick and Quebec than elsewhere (Table IV). Non-resident anglers from the United States were most frequently from Massachusetts, New York and New Hampshire while smaller percentages were from other states (Table V).

Fishing Gear and Angling Success

Resident and non-resident anglers regardless of location most frequently angled with bait. Bait angling was more common on Scales Pond than in the Lower Dunk River. In most cases, the bait consisted of live earthworms, but corn, pieces of cooked mackerel, live smelts, and killifish were also used.

Resident bait fishermen angling in the Lower Dunk River caught a much smaller percentage of the total catch (62.8-69.4% for the brook trout and 52.3-75.5% for

Table II. Summary of the number of rainbow trout stocked in the Dunk River system

Year	Source	Number of trout stocked in the Dunk River system
1941	Cape Cod	18,000
1954	U.S.A.	8,000
1955	U.S.A.	15,400
1957	St. John, N.B.	5,000
1958	U.S.A.	5.000
1959	U.S.A.	6,000
1961	U.S.A.	7,800
1963	Cape Breton Island	12,540
1964	St. John, N.B.	10,000

Table III. Summary of the number of fishermen interviewed and the distance they travelled to fish in the Dunk River system

			Number of fishermen interviewed and distance travelled			
Year	Area		0-5 km	5.1-10 km	10.1-20 km	20 km
1973	Lower Dunk River		125	31	927	48
	Scales Pond		52	2	202	24
		Total	177	33	1129	72
1974	Lower Dunk River		76	56	1304	99
	Scales Pond		45	20	524	69
		Total	121	76	1828	168
1975	Lower Dunk River		96	59	783	72
	Scales Pond		25	13	318	50
		Total	121	72	1101	122

rainbow trout) than those on Scales Pond (82.7-93.2% for brook trout and 78.6-90.5% for rainbow trout). Fly fishermen were generally more successful in catching trout in the Lower Dunk River than in Scales Pond. Regardless of gear, however, resident fishermen were consistently more successful, as determined by cach per trip, than non-resident anglers. Knowledge of the river and of local angling techniques pobably accounted for this difference in success.

Fishing Pressure per Hectare and Catch per Hour

Fishing pressure in the Lower Dunk River area (Table VI) during the summer months fluctuated between 50.9 and 143.2 hours/hectare with higher fishing pressure in the late spring than in the late summer. Resident and non-resident anglers expended 3,017 to 4,971 hours/season. Catch per hour values changed irregularly and did not always vary directly with fishing pressure. Regardless of area or month, anglers always caught more brook trout per hour than rainbow trout.

The estimates of fishing pressure and catch per hour values for Scales Pond (Table VII) were markedly lower than those for the Lower Dunk River. The extremely low values for July and August in 1975 were due to a lowering of the water level in Scales Pond to permit construction of a fish ladder at the dam. Reduction in the pond volume uncovered the accumulated soft-bottom sediments and prevented

Table IV. Number of non-resident fishermen interviewed from Canada, angling on the Dunk River between 1973 and 1975. Percentages are shown in parentheses

	1973	1974	1975
New Brunswick	21(17.5)	70(26.8)	15(12.9)
Nova Scotia	32(26.7)	60(23.0)	34(29.3)
Newfoundland	-	2(0.8)	1(0.9)
Quebec	14(11.7)	42(16.1)	28(24.1)
Ontario	46(38.2)	81(31.0)	36(31.0)
Manitoba	3(2.5)	-	1(0.9)
Saskatchewan	-	1(0.4)	-
Alberta	2(1.7)	3(1.1)	1(0.9)
British Columbia	2(1.7)	2(0.8)	-
Total	120(100)	261(100)	116(100)

Table V. Number of non-resident fishermen interviewed, from the United States and abroad, angling on the Dunk River between 1973 and 1975. Percentages are shown in parentheses.

	1973	1974	1975
New York	16 (21.7)	5 (7.8)	6 (21.4)
Wash. D.C.	2 (4.3)	-	-
Massachusetts	20 (43.5)	22 (34.4)	12 (42.8)
N. Carolina	1 (2.2)	-	-
Tennessee	1 (2.2)	-	4 (14.3)
New Hampshire	8 (17.4)	2 (3.1)	-
Maine	2 (4.3)	5 (7.8)	2 (7.7)
Indiana	1 (2.2)	-	-
California	1 (2.2)	1 (1.5)	-
Iowa	-	2 (3.1)	-
Arizona	-	1 (1.6)	-
New Jersey	-	9 (14.1)	-
Pennsylvania	-	2 (3.1)	-
Ohio	-	1 (1.6)	-
Connecticut	-	2 (3.1)	3 (10.7)
Vermount	-	2 (3.1)	
Virginia	-	1 (1.6)	
Unknown	-	9 (14.1)	-
France			1 (3.6)

Table VI. Summary of the estimated fishing pressure in hours per hectare and mean catch per hour by resident and non-resident fishermen on the Lower Dunk River between May 7 and September 3, 1973 to 1975.

	1973				1974				1975			
Period	Fishing pressure ($h\ ha^{-1}$)	Mean Catch per hour			Fishing pressure ($h\ ha^{-1}$)	Mean catch per hour			Fishing pressure ($h\ ha^{-1}$)	Mean catch per hour		
		BK[1]	RB[2]	Total		BK	RB	Total		BK	RB	Total
May 7-June 5	142.6	0.71	0.06	0.77	143.2	0.61	0.08	0.69	91.4	0.37	0.05	0.42
June 6-July 5	83.6	1.05	0.10	1.15	135.6	0.57	0.07	0.64	94.1	0.81	0.11	0.92
July 6-Aug. 4	63.0	0.55	0.19	0.64	100.8	0.53	0.10	0.64	50.9	0.75	0.17	0.92
Aug. 5-Sept. 3	53.0	0.60	0.10	0.70	99.4	0.38	0.08	0.46	53.8	0.63	0.32	0.95

[1] Brook trout [2] Rainbow trout

Table VII. Summary of the estimated fishing pressure in hours per hectare and mean catch per hour by resident and non-resident fishermen on Scales Pond between May 7 and September 3, 1973 to 1975.

	1973				1974				1975			
Period	Fishing pressure ($h\ ha^{-1}$)	Mean catch per hour			Fishing pressure ($h\ ha^{-1}$)	Mean catch per hour			Fishing pressure ($h\ ha^{-1}$)	Mean catch per hour		
		BK[1]	RB[2]	Total		BK	RB	Total		BK	RB	Total
May 7-June 5	19.8	0.19	0.05	0.24	35.4	0.46	0.07	0.53	36.4	0.33	0.03	0.36
June 6-July 5	13.8	0.40	0.11	0.51	36.4	0.35	0.06	0.41	22.7	0.37	0.04	0.41
July 6-Aug. 4	9.7	0.53	0.02	0.55	21.9	0.47	0.04	0.51	0.3	4.60	0.30	4.90
Aug. 5-Sept. 3	10.0	0.16	0.07	0.23	25.7	0.41	0.07	0.48	0.6	1.18	0.32	1.40

[1] Brook trout [2] Rainbow trout

fishermen from angling. As a result, fishing pressure declined and abnormal catch per hour values were recorded.

Angler Harvest

Estimates of resident angler harvest (Table VIII) in the Lower Dunk River for the study years ranged between 164 and 245 brook trout/hectare (18.3-23.6 kg ha^{-1}) and between 30 and 36 rainbow trout (6.0-6.7 kg ha^{-1}). In comparison, non-resident anglers harvested between 11 and 19 brook trout/hectare (1.1-2.1 kg ha^{-1}) and 3 to 5 rainbow trout (0.3-0.9 kg ha^{-1})/season.

In all years, there was a greater number of resident fishermen in the Lower Dunk River area between May 7 and July 5 than at any other time, probably stimulated by upriver movements of native trout from the estuary. Decreased angling activity in late summer was probably related to poorer catches due to low and warmer water.

During the study period resident anglers at Scales Pond (Table VIII) expended 1,009 to 2,399 hours/season and took 15 to 106 brook trout/hectare (1.2-4.0 kg ha^{-1}) and 2 to 7 rainbow trout/hectare (0.5-1.3 kg ha^{-1}). Non-resident anglers fished 40 to 407 hours and harvested 1 to 4 brook trout/hectare (0.1-0.3 kg ha^{-1}) and 0.2 to 0.7 rainbow trout/hectare (0.04-0.2 kg ha^{-1}).

Catch by Area

The study areas were mapped and divided into sections (Fig 1) so that the approximate capture locations could be determined. About 35% of all brook trout and 30% of all rainbow trout were caught in the region just below Scales dam (section 17) with other major catches occurring in deep pools in the river sections with tributaries (sections 9 and 11). Most of the trout harvested in Scales Pond were angled near the dam (sections 18 and 19) where the water was deeper and generally cooler than in upsteam sections.

Size of Trout Harvested

Both groups of anglers most frequently caught trout that ranged in size between 15.0 and 30.0 cm in fork lengths and in age between 2 and 4 years. Anglers caught very few brook trout older than 4+ years; however, a slightly larger number of older rainbow trout were caught in both areas.

Number of Trout Creeled per Fishing Trip

The number of fishermen catching more than 5 trout/trip in the sample of fishermen interviewed was small in comparison to those catching beween 1 and 5 trout/trip. The number of fishermen catching more than 10 trout/trip was large for resident anglers, particularly in the Lower Dunk River. These fishermen, while few in number in comparison to the other groups, harvested almost as many trout as those catching 1 or 2 trout/trip.

Population Estimates

Populations were estimated for the Lower Dunk River area between Johnston's Bridge and the dam at Scales Pond in August of 1973 and 1974 (Table IX).

Poor sampling of 0+ and 1+ trout is the most likely cause for their low estimates in 1973, since 1+ and 2+ trout in 1974 were abundant. Also, trout tagged in the tributaries, North Brook, and Southwest Brook were later recaptured in the Lower Dunk River and similarly, trout tagged in the Lower Dunk River were later recaptured in the tributaries in the fall prior to spawning. However, the extent of recruitment to or loss from trout populations in the Lower Dunk River cannot be accounted for in these estimates.

Table VIII. Estimated catch of native brook trout and rainbow trout by resident and non-resident fishermen angling in the Lower Dunk River and Scales Pond between May 7 and Sept. 3, 1973 to 1975. Numbers in parentheses under each total are estimated weights for the estimated numbers of trout caught and are based on weighed samples

		Estimated harvest + 1 S E							
		Lower Dunk River				Scales Pond			
Stratum	Year	Brook trout		Rainbow trout		Brook trout		Rainbow trout	
		Res.[1]	Non-res.[2]	Res.	Non-res.	Res.	Non-res.	Res.	Non-res.
May 7	1973	1018 ± 69	22 ± 12	84 ± 14	2 ± 1	77 ± 15	12 ± 6	22 ± 7	0
to	1974	872 ± 82	27 ± 12	118 ± 31	2 ± 2	371 ± 64	15 ± 10	55 ± 15	5 ± 4
June 5	1975	344 ± 36	0	44 ± 10	0	285 ± 52	0	24 ± 4	0
June 6	1973	864 ± 93	29 ± 16	81 ± 11	6 ± 3	131 ± 29	0	35 ± 8	0
to	1974	758 ± 55	33 ± 16	97 ± 11	4 ± 3	292 ± 39	12 ± 9	56 ± 13	0
July 5	1975	778 ± 87	4 ± 2	103 ± 12	0	199 ± 42	0	21 ± 7	0
July 6	1973	307 ± 50	48 ± 14	89 ± 8	33 ± 9	112 ± 30	10 ± 6	5 ± 2	0
to	1974	487 ± 39	57 ± 27	83 ± 10	19 ± 11	213 ± 37	28 ± 8	23 ± 5	0
Aug. 4	1975	252 ± 53	135 ± 51	57 ± 7	57 ± 7	30 ± 14	0	2 ± 1	0
Aug. 5	1973	314 ± 641	10 ± 3	51 ± 6	4 ± 1	31 ± 16	8 ± 3	12 ± 4	5 ± 1
to	1974	310 ± 51	73 ± 13	74 ± 8	5 ± 2	209 ± 35	40 ± 13	31 ± 13	11 ± 3
Sept. 3	1975	303 ± 29	44 ± 21	158 ± 23	16 ± 15	18 ± 17	0	5 ± 4	0
	1973	2503 ± 253 (240.82)[3]	109 ± 45 (11.32)	305 ± 39 (68.73)	45 ± 14 (3.96)	351 ± 90 (27.05)	30 ± 15 (3.34)	74 ± 21 (11.25)	5 ± 1 (0.85)
Total	1974	2427 ± 227 (224.61)	190 ± 68 (17.03)	372 ± 60 (61.27)	30 ± 18 (3.25)	1085 ± 175 (95.00)	95 ± 40 (7.73)	165 ± 46 (31.42)	16 ± 7 (3.59)
	1975	1677 ± 205 (186.29)	183 ± 74 (21.44)	362 ± 52 (63.21)	49 ± 32 (9.19)	532 ± 125 (56.75)	0	52 ± 16 (15.88)	0

[1] resident fishermen [2] non-resident fishermen [3] kilograms

Table IX Estimates of the number of native brook trout and rainbow trout in the Lower Dunk River populations in August 1973 and 1974. Standard errors are shown for each total.

Species	Date of estimate	Estimates of the number of trout in each age class (yr) 0+	1+	2+	3+	4+	5+	Total
Brook Trout	Aug. 1973	2295	1311	2090	451	37	-	6184 ±1007
	Aug. 1974	12096	6431	5255	998	210	22	25012 ±1722
Rainbow Trout	Aug. 1973	49	597	294	59	-	-	999 ±63
	Aug. 1974	2600	417	587	139	32	6	3781 ±200

Table X. Summary of the estimated angler's harvest and population size of native brook trout and rainbow trout in the Lower Dunk River in 1973 and 1974

Species	Year	Angler harvest of 1+ trout	Angler harvest[1]	Population	Pre-May population size[1]	Exploitation rate of pre-May population[1]
Brook trout	1973	242	2370	2578	4948	0.48
	1974	381	2236	6485	8721	0.26
Rainbow trout	1973	34	316	353	669	0.47
	1974	27	375	764	1139	0.33

[1] 2+ and older trout

Estimates of population biomass (0+ and older) in 1973 were 294 kg brook trout (28.3 kg ha^{-1}) and 55 kg rainbow trout (5.3 kg ha^{-1}); in 1974 these were 980 kg brook trout (94.3 kg ha^{-1}) and 158 kg rainbow trout (15.2 kg ha^{-1}).

Exploitation Rates

The exploitation rates of the precensused brook trout and rainbow trout populations (2+ and older) are presented in Table X. Since small numbers of 1+ brook trout and rainbow trout were creeled by anglers and since 1+ population estimates were low, the final estimates of harvest and population size were adjusted to account only for 2+ and older trout.

Discussion

Total estimated harvests of brook trout and rainbow trout varied little between years. Unfortunately, there are few other studies for Prince Edward Island with which to compare the minimum yield data for the Lower Dunk River and Scales Pond. Most earlier reports concern only brook trout in pond environments (Smith 1951; 1963; Saunders & Smith 1968) and there is nothing on the harvest of rainbow trout. Annual yields of brook trout from Scales Pond were much lower than the 20.0 to 39.2 kg/hectare for Montague Pond in eastern Prince Edward Island (Smith 1951) or 13.6 to 20.6 kg/hectare for Wilmot Pond in central Prince Edward Island (Smith 1963) or 8.0 to 50.2 kg/hectare for Ellerslie Pond in western Prince Edward Island (Saunders & Smith 1968). Persistently low yields suggest that only a small population of trout occurs in Scales Pond, and this is believed to be caused by unsuitable trout habitat. In July 1975, when the water level in the Pond was reduced for construction of a fish ladder at the dam, it became apparent that the pond basin was heavily silted (0.25-1.00 m thick) with few aquatic plants and other suitable hiding places on bottom. The lack of suitable hiding places and silting have been found to affect the carrying capacity and harvest in other Prince Edward Island localities (Saunders & Smith 1962; 1968; 1965; Smith 1963).

Information on yields and standing crops of brook trout in other coastal river environments of Prince Edward Island is also scarce. Saunders and Smith (1955) reported that the mean biomass of the standing crop of brook trout in Hayes Brook was 151.8 kg/hectare, considerably higher than the 28.2 to 86.0 kg/hectare for the Lower Dunk River area. Hayes Brook is the smaller system, less open, with more cover and less silting. The Lower Dunk River also supports 3 species of salmonids which may compete for food, living space and spawning sites.

While standing crops in the Dunk River system were lower than elsewhere, exploitation levels for 2+ and older trout (0.28-0.49) were equal to or greater than those reported by Smith and Saunders (1968) for the Ellerslie stream (0.11-0.34). Exploitation rates for brook trout in Lower Dunk River were high in 1973, but lower catches in 1974 did not occur. Instead, higher catches and lower exploitation levels were recorded, suggesting a higher trout density. This higher trout density could have occurred only as a result of recruitment from the Pond or, most probably, from the estuary. Our observations on a 905-m section of the North Brook suggest that trout move into this tributary in the fall and leave it in winter, spring or early summer. Tributaries appear to be important nursery areas and important sources of trout, and their role in sustaining the fishery in the more heavily fished zones of the Dunk River system needs to be evaluated.

Unlike brook trout, rainbow trout are not as easily caught and, based on catch data for all years, many more older trout existed in their population. Our results add to Gard and Seegrist's (1972) findings that rainbow trout are harder to catch than brook trout. It appears that rainbow trout provide a more diversified and higher quality fishing experience even though total standing crop may be less than that for single species fishery.

Management Implications

In the Dunk River, as in the Ellerslie system (Smith & Saunders 1968), anglers substantially exploit native brook trout populations below impassable dams where migratory sea trout concentrate. At present, there are no regulations in Prince Edward Island controlling the harvest of trout from these areas. Excessive cropping of larger, older trout leaves only the smaller trout to reproduce, and possibly increases genetic selection in favour of smaller, shorter-lived, non-sea-running stocks. Johnston and McKenna (1976) have shown that older sea trout produce a greater number of larger eggs than do smaller trout. Larger eggs produce larger fry that are more robust and more able to survive in highly competitive environments (Svardson 1949). High standing crops of trout in Island waters appear to be related in part to older sea trout in the population, and any management strategy should attempt to ensure their presence.

In this study most brook trout caught by fishermen or captured in population estimates were less than 4 years old. While studies elsewhere have demonstrated that creel limits are ineffective in allowing fish to survive to an older age (Hunt 1964; Latta 1973; Shetter 1967), our data suggest that approximately 20% of the trout angled would not have been harvested if the creel limit of 20 had been reduced to 10 brook trout/day and if the angling pressure remained the same as during the study.

While little is known about the potential carrying capacity of Island streams and ponds, it would appear that the Dunk River system is below this potential. Excessive sedimentation by soil erosion from nearby fields and roads seems to be the most important limiting factor. Stewart and Himelman (1974) studying soil erosion in the Dunk River watershed, estimated that during snow melt in April up to 16.4 t/acre are eroded. If salmonid populations in Island waters are to be enhanced, programs of soil erosion abatement and habitat rehabilitation must be implemented to improve ponds, streams and estuaries.

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ENDOLITHIC FAUNA OF VACATED ZIRFAEA CRISPATA L. BURROWS IN BLOMIDON SHALE, MINAS BASIN, NOVA SCOTIA

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At Cape Blomidon, Minas Basin, there are numerous vacated *Zirfaea crispata* burrows in the shale terraces exposed at low tide. About 300 burrows were flushed of sediments and screened for fauna. Eighty-eight species were identified and 16 are new records for Minas Basin. Of the 654 specimens, 67% were attributable to 1 burrowing anemone, 4 gastropods, 3 amphipods, and 3 genera of polychaetes. A group of 11 polychaete species, of the 34 species collected, accounted for 76% of all polychaetes and for 42% of the entire collection.

Introduction

The great piddock clam, *Zirfaea crispata* L., burrows in peat, clay and soft rocks, usually sublittorally, but can occur in the lower eulittoral (Allen 1969; Abbott 1974; Gosner 1979). It ranges from Labrador to New Jersey and along the west coast of Europe but has not previously been reported from Minas Basin. In areas such as Minas Basin which experience daily macrotidal cycles (about 16 m), a band of the lowest eulittoral and adjacent sublittoral fringe can become exposed on certain extreme low-water tides (Bleakney 1972). At this level we have found active *Zirfaea crispata* aggregations, some of which occur as high as 110 cm above chart datum, in Cape Blomidon shales. In contrast, on the Northumberland coast of England (Allen 1969) they extended only 20 cm above datum.

Successive generations of this large pholad (valve dimensions 5.5 x 3.5 cm) have pitted the series of nearly horizontal shale terraces (5° dip to NW) with vertical inverted-cone-shaped burrows in densities up to 158/m^2 although most areas range between 22 and 75 burrows/m^2. As the individual *Zirfaea* lives but 5 to 7 years (Allen 1969) and the rock erodes at a mere 0.01 to 0.05 cm/yr (unpublished data, Bleakney), the original 18 to 22 cm-deep burrows are available for occupancy by other organisms for hundreds of years after the original excavators have died. The age of many burrows can be dated by ^{14}C determination of the entrapped *Zirfaea* valves. One burrow at station No. 6 (Fig 1) was 9 cm deep and the extracted shell was dated 865 (± 100) yr B.P. (Dal-318, Dalhousie University Radiocarbon Lab). In terms of life spans of marine invertebrates, these burrows represent a permanently available minihabitat.

A majority of the burrows in the lower eulittoral and sublittoral fringe are not occupied by live *Zirfaea*. They contain 2 empty tight-fitting valves at the bottom and are otherwise filled with accumulated sediments and detritus captured from the water column which because of the macrotidal cycles is turbid with suspended organic and inorganic particles (Amos 1977). From September 1978 to February 1979 the burrows in this area were periodically sampled to determine if the infauna of these sediment cylinders in a rocky shore was the same as that in the contiguous, broad intertidal flats of the western Minas Basin. The latter were intensively surveyed by Gratto (1978) at 930 sampling stations. A total of 88 taxa was eventually extracted from the *Zirfaea* burrows, 16 of which are additions to the reported fauna of Minas Basin and 55 of which were not recorded in Gratto's list of 76 species.

During this preliminary survey such groups as Protozoa, Nematoda, Kinorhyncha, Copepoda, and Ostracoda could not be considered.

As this is the first study of endolithic fauna of vacated *Zirfaea* burrows, no geographic comparisons were possible. Evans (1967) working with *Penitella penita* in Oregon made incidental mention of other organisms in pholad burrows but only by general category (coelenterates, annelids, sipunculoids, crustaceans, molluscs, and urochordates), not by species. Morton (1973) stated that terebellids, cirratulids, and nerids occupy vacated burrows of New Zealand pholads.

Study Area and Methods

The geology of the study area (45°15.6′N, 64°20.2′W) has been described by Crosby (1962) as an outcrop of Blomidon shale dipping 5° to the northwest and composed of soft brick-red shale and argillaceous sandstone that is continually eroding away. The slight inshore tilt of the shale terraces creates long shallow pools as evident in Figure 1. Sea surface temperatures at Cape Blomidon taken at low tide at nearly monthly intervals from April 1977 to February 1979 varied from a high of 17.5° to a low of –1.5°C. Salinities were stable near 29‰ and suspended sediment loads ranged from 1.5 to 3 mg/*l* (Pennachetti 1978). Tidal range varies from about 11 m to 14 m and longshore currents sweep the terraces making it extremely difficult to anchor over the area even during "slack" high tide. Macroalgae are generally sparse on these Cape Blomidon terraces but *Chondrus crispus, Gigartina stellata, Corallina officinalis,* and *Lithothamnion* spp. were the most conspicuous near low water.

A transect with sampling stations was established from the uppermost *Zirfaea* burrows to extreme low water (Fig 1), a horizontal distance of about 51 m and a vertical distance of about 135 cm. Stations No. 1 (*Petricola pholadiformis* burrows only)

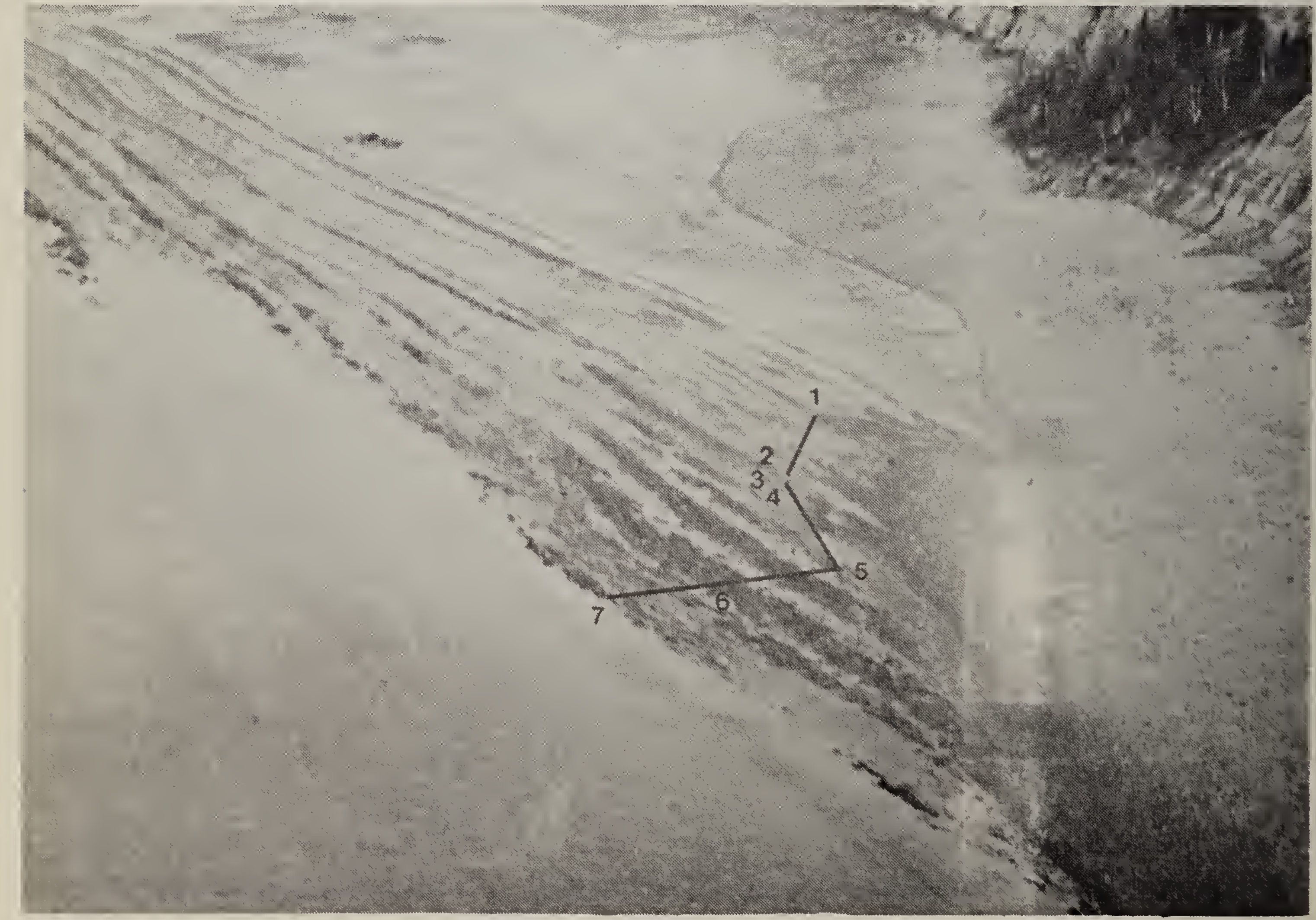

Figure 1. Air photo of Cape Blomidon shale terraces and pools with the transect line and survey stations, at a 0.2 m tide.

and No. 2 were unproductive in terms of endolithic fauna so this report concerns only stations No. 3 to No. 7. The position of the stations relative to each other and to a sample of tidal predictions is plotted in Table II as well as the average depth of burrows measured at each station level.

As the study area was exposed only for a few days each lunar month, only 10 field trips were completed over the 6-month period. In order to sample as many burrows as possible over the brief exposure times, a flushing apparatus was constructed which removed burrow contents with minimal damage to delicate burrowing organisms. A 3.7 cm diameter perspex cylinder 20 cm long was tightly positioned over each burrow and a stream of water from a small bilge pump hosed into the burrow. The overflow was directed out a spout at the side of the cylinder into a coarse sieve (3560 μm mesh apertures) and fine sieve (351 μm). After several burrows were flushed the sieves were separated, the contents washed, placed in separate jars, and another series of flushings begun. One hundred and nineteen of the flushed burrows were measured for depth and diameter for determination of average burrow size at each station level (Table I). Initially the contents of each burrow were kept separate, the burrow measured and its volume determined by measuring its water volume in a graduated cylinder. However, as manpower was limited and few burrows could be processed on a tidal cycle in this detail, the emphasis was shifted to simply obtaining a mass sample from burrows of all sizes and thereby assuring a collection representative of species present. Burrows were then flushed randomly and rapidly in the vicinity of each station. As the burrows were of different volumes and this could not be measured under the circumstances, no record unfortunately was kept of grand total actually sampled. However, with volume determinations of burrows 3, 6, and 10 cm in depth and knowing the average burrow depth at each station, we have roughly estimated the number of burrows flushed at each station and calculated the volumes of substrate sieved (Table I).

The approximate volume of substrate sampled is relatively small when compared with Gratto's efforts (1978). Along each of his 221 transects 700 ml were sieved at each station and by mid-August he had processed 930 samples (ca. 651,000 ml) and identified 76 species.

Results and Discussion

The species and numbers of specimens collected at each station are listed in Table III. From the total 654 specimens extracted from the estimated 300 burrows, 88 species were identified of which 16 had not previously been reported from Minas

Table I. Estimate of volume of burrow sediments sieved at each station based on measurements of 119 burrows.

Station Number	Estimated Flushed Burrows	Average Depth	Average vol/burrow	Total Substrate Sieved
3	20	3.7 cm	40 ml	800 ml
4	40	5.7	60	2400
5	80	5.7	60	4800
6	80	7.9	80	6400
7	80	8.1	80	6400
	300			20800 ml

Table II. Vertical distances between collecting stations and estimated Chart Datum at Cape Blomidon. Tidal predictions in meters are from Saint John, N.B. tables and are therefore only relative. The tides of February and March were atypical when compared with the October to January series.

Tidal Height (cm)	Station No.	Vert. Diff. (cm)	Tidal Prediction and Tidal Observation (m)	Avg. Depth of Burrows at Stations (cm)
110	3			3.7 (n=3)
100		19		
90	4			5.7 (n=33)
80		16		
	5			5.7 (n=43)
			0.4 Oct 4 '78	
70				
		16		
60				
	6			7.9 (n=14)
			0.3 Nov 1 '78	
50				
		23		
40				
	7			8.1 (n=18)
			0.24 Nov 2 '78	
30			0.2 July 10 '79	
			0.36 Mar 27 '79	
20				
			0.09 Dec 1 '78	
			0.18 Feb 28 '79	
10			0.06 Jan 27 '79	
			0.03 Sept 8 '79	
0	estimated Chart Datum			

Table III. List of 88 species collected from vacated *Zirfaea crispata* burrows at Cape Blomidon, Nova Scotia. **Sixteen new records for Minas Basin. *Fifty-five species additional to Gratto's 1978 eulittoral survey.

	Stations					
	3	4	5	6	7	Totals
Phylum: CNIDARIA (2 species, 12 specimens)						
***Edwardsia elegans* Verrill				4	7	11
***Tealia felina* (Linnaeus)				1		1
Phylum: NEMERTINEA (6 species, 16 specimens)						
*unidentified species					2	2
*unidentified species					3	3
Lineus sp.				4		4
Cerebratulus sp.				2	2	4
Amphiporus sp.					1	1
*unidentified species				1	1	2
Phylum: MOLLUSCA (23 species, 204 specimens)						
**Ischnochiton ruber* (Linnaeus)					2	2
**Acmaea testudinalis* (Muller)	1			1	1	3
**Lacuna vincta* (Montagu)	1			31	26	58
**Littorina littorea* (Linnaeus)	6	1	27	12	5	51
**Crepidula fornicata* (Linnaeus)				4	16	20
**Mitrella lunata* (Say)		1		7	7	15
Nassarius trivittatus (Say)			1	4		5
***Admete couthouyi* (Jay)		1		2	2	5
**Lora bicarinata* (Couthouy)				2		2
**Acanthodoris pilosa* (Muller)				3		3
**Nucula proxima* Say					3	3
**Musculus corrugatus* Stimpson					1	1
**Crenella glandula* (Totten)				3	1	4
**Astarte castanea* Say					1	1
Gemma gemma (Totten)		1	1			2
Petricola pholadiformis Lamarck				6	2	8
Macoma balthica (Linnaeus)					1	1
Ensis directus Linnaeus					3	3
**Hiatella arctica* (Linnaeus)				6		6
Mya arenaria Linnaeus	1	1	1			3
***Zirfaea crispata* (Linnaeus)				3	2	5
**Pandora gouldiana* Dal					1	1
**Lyonsia hyalina* (Conrad)				1	1	2
mollusca subtotals	9	5	30	85	75	204
	3	4	5	6	7	Totals
Phylum: ANNELIDA (34 species, 277 specimens)						
***Harmothoe extenuata* (Grube)					2	2
**Harmothoe imbricata* (Linnaeus)				5	9	14
**Lepidonotus squamatus* (Linnaeus)				1	4	5
Eteone longa (Fabricius)				2	5	7
***Eulalia viridis* (Linnaeus)				1	2	3

**Phyllodoce groenlandica* Oersted				1	12	13
**Phyllodoce maculata* (Linnaeus)			3	12	17	32
Phyllodoce mucosa Oersted	1		1	3	10	15
Exogone dispar (Webster)				2	2	4
**Exogone hebes* (Webster and Benedict)					3	3
Nereis virens Sars	1		2	1	3	7
**Aglaophamus neotenus* Noyes			2	4	5	11
Nephtys caeca (Fabricius)				3	4	7
***Stauronereis caeca* (Webster and Benedict)				1	2	3
Lumbrineris fragilis Muller			1			1
Aricidea succica Bliason				1	1	2
Polydora ligni Webster			1	1		2
**Scolelepis squamata* (Muller)					1	1
Spio filicornis (Muller)					4	4
Streblospio benedicti Webster				1		1
Chaetozone setosa Malmgren				2	8	10
***Cirratulus cirratus* (Muller)				2		2
**Tharyx acutus* Webster and Benedict			1	2	1	4
***Pherusa affinis* (Leidy)					1	1
Heteromastus filiformis (Claparede)			1	1		2
***Notomastus latericeus* Sars			1	1		2
Clymenella torquata (Leidy)			2	27	10	39
Clymenalla zonalis (Verrill)				10	26	36
***Praxillella* sp.			1			1
**Sabellaria vulgaris* Verrill					2	2
**Amphithrite figulus* (Dalyell)				5	6	11
***Polycirrus phosphoreus* Verrill				12	1	13
***Nicolea venustula* (Montagu)				1		1
***Potamilla reniformis* (Leukart)				2	14	16
annelida subtotals	2	0	16	104	155	277

Phylum: SIPUNCULA

	3	4	5	6	7	Totals
***Phascolopsis gouldi* (Pourtalès)				1	1	2

Phylum: ARTHROPODA (Crustacea) (18 species, 130 specimens)

Oxyurostylis smithi Calman			1		1	2
Leptognathia caeca (Harger)				1		1
Chirodotea caeca (Say)				1		1
Idotea phosphorea Harger				1	1	2
Jaera marina (Fabricius)				1		1
**Ampithoe rubricata* Montagu			1	7	7	15
**Leptocheirus pinguis* (Stimpson)				2	1	3
**Unicola irrorata* Say				1		1
Corophium bonelli (Milne-Edwards)				29	5	34
Corophium volutator (Pallas)				3	2	5
Gammarus lawrencianus Bousfield		6				6
**Bathyporeia quoddyensis* Shoemaker				1		1
***Harpinia propinqua* Sars					1	1
**Phoxocephalus holbölli* (Krϕyer)				19	17	36
**Pontogeneia inermis* (Krϕyer)				11		11
Crangon septemspinosa Say			1		1	2

Pagurus acadianus Benedict				5	2	7
**Cancer irroratus* Say				1		1
arthropoda subtotals		6	3	83	38	130
Phylum: ECHINODERMATA						
**Leptasterias tenera*					3	3
**Amphipholis squamata* (Delle-Chiaje)					4	4
Phylum: HEMICHORDATA						
**Saccoglossus kowalewskii* (Agassiz)			1	2	2	5
Phylum: CHORDATA						
**Molgula citrina* Alder and Hancock				1		1
Total individuals	11	11	50	288	294	(654)
Total species	6	6	19	62	63	(88)

Basin. Only 33 of these species occurred also in samples from local inter-tidal flats (Gratto 1978). However, such a direct comparison must be qualified by noting that Gratto's transects did not extend to extreme low water and all his samples were from sand and mud, none from rock surfaces or crevices. Many of the *Zirfaea* burrow species are typical of crevice cryptofauna (anemone *Tealia,* several gastropods, isopods, decapods, many polychaetes, and small echinoderms) or are small juveniles of large species that the burrows could not accommodate at the adult stage (*Mya arenaria, Ensis directus, Crepidula fornicata, Macoma balthica).* The paucity of individuals of the species in these categories indicates their incidental utilization of vacated *Zirfaea* burrows.

Another evident group is the typical cold water and/or deeper sublittoral species (*Admete couthouyi, Lora bicarinata, Lacuna vincta, Mitrella lunata, Astarte castanea, Nucula proxima, Crenella glandula)* which have been able to move up to this tidal level firstly because of the lack of temperature stratification (resulting from macrotidal mixing in the Basin) and secondly because of the "subtidal" environmental stability afforded by these burrows. It seems unlikely that during periods of tidal exposure the salinity or temperature in burrows could be altered nor would wave action disturb their contents.

It is evident from Table II that the area of deeper burrows within 60 cm of chart datum is best suited to the development of an endolithic community. Although there are actually more burrows per unit area near station No. 5 and much survey effort was concentrated there, 89% of all specimens extracted came from stations No. 6 and No. 7 (with a near equal distribution, Table III). Similarly, 94% of the 88 species were recorded at those 2 levels and only 5 species were limited to the upper stations No. 3, No. 4, and No. 5.

Considering only stations No. 5, No. 6, and No. 7, one can recognize a community of species which are consistently present in the samples. Employing the usual mystical arbitrary figure of species with 10 or more specimens represented in the survey, these dominant forms are: 1 burrowing anemone *(Edwardsia elegans),* 4 gastropods which together constitute 22% of all specimens *(Lacuna vincta, Littorina littorea, Crepidula fornicata, Mitrella lunata),* 4 amphipods which constitute 15% *(Ampithoe rubricata, Corophium bonelli, Phoxocephalus holbölli, Pontogeneia inermis),* and 11 polychaetes which constitute 32%. These 11 polychaetes also account for 76% of all polychaete specimens.

Of the 4 gastropods, only *Lacuna vincta* is dominant as an adult, the 3 other species being represented by small individuals. The 4 dominant amphipods are 2 tube dwellers, *Ampithoe rubricata* and *Corophium bonelli,* a burrower *Phoxocephalus holbölli,* and one collection of the free-living phycophilic *Pontogeneia inermis,* the latter possibly a sampling anomaly. The 2 *Corophium* species are of particular interest because from the adjacent intertidal flats Gratto (1978) obtained counts of *C. volutator* over 300/m^2 but never a *C. bonelli.* It would be interesting to know if the 2 species could occur in the same *Zirfaea* burrow.

Polychaete collections from transects along 40 km of western Minas Basin tidal flats were analysed by McCurdy (1979). He reported 72% of all eulittoral polychaete specimens (42 species) were attributable to only 3 species: *Heteromastus filiformis, Chaetozone setosa,* and *Streblospio benedicti.* However, in the nearby *Zirfaea* burrows these species are rare (4.6% of total) and instead 3 species of *Phyllodoce* and 2 species of *Clymenella* make up 49% of the polychaete sample. A more interesting comparison is to recognize the unusual situation of 11 predominant species whose total numbers account for 76% of all polychaetes collected.

The endolithic community of vacated *Zirfaea* burrows at Cape Blomidon differs from other communities surveyed thus far in Minas Basin (Gratto 1977; 1978; Fuller & Trevors 1977; Bromley 1978; Yeo 1978; McCurdy 1979). The burrow fauna probably represents a sample of the smaller species that are typical in general of the sublittoral fringe zone of the western Minas Basin. Vacated pholad burrows in themselves represent a unique and presumably extensive Atlantic coast habitat not previously examined.

Summary

At Cape Blomidon, Minas Basin, the shale terraces exposed during extreme low water tides are pitted with vacated burrows of the great piddock clam *Zirfaea crispata.* The accumulated sediments in vacated burrows were flushed and sieved. An endolithic faunal sample of 654 specimens was obtained and totalled 88 species of which 16 are new records for Minas Basin.

The predominant species, together constituting 67% of all specimens, were 1 burrowing anemone, 4 gastropods, 3 amphipods, and 2 genera (5 species) of polychaetes none of which is a dominant species in the adjacent extensive intertidal flats of western Minas Basin.

A group of 11 polychaete species accounted for 76% of all polychaete specimens and for 42% of the entire collection.

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THE EFFECT OF STORAGE ON THE ENERGY VALUES OF SOME PLANT AND ANIMAL MATERIAL

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Both plant and animal tissues were stored for extended periods of time to determine the effect on energy value. Animal tissues were found to have significantly lower calorific content after 7 to 10 mo storage in covered petri dishes at -15°C, but significant differences were not detected in the energy values of plant tissue after storage for 1 yr in a desiccator at 20°C.

Introduction

Recent literature is replete with data on the energy content of ecological material (see Cummins & Wuycheck 1971), but to date there appears to be no information about the effect of storage on such determinations. Parr Manufacturing Co. (cited in Paine 1971) recommends a period not exceeding 30 days between collection and combustion; however, no empirical evidence to support this is presented. Because time limitations may prevent ecologists from processing their material this rapidly, baseline data on the effects of prolonged storage on the energy value are needed. This note is a report of such data.

Materials and Methods

The energy values of isopod tissue *(Idotea baltica)* and blueberries *(Vaccinium § Cyanococcus)* collected at various times of the year were determined by microbomb calorimetry following methods outlined elsewhere (Strong & Daborn 1978). Carbonate corrections were not necessary for blueberrs tissue and all energy values are expressed as J/mg-dry weight**. Both isopods and blueberries were stored as pellets, the former at -15°C in loosely covered petri dishes for 7 to 10 months, and the latter in a desiccator at 20°C for 12 months. Consequently it cannot be assumed that the isopod tissue remained dry during storage. The statistical significance of the changes in mean energy value was examined with a Student's *t*-test.

Results and Discussion

The results are presented in Table I. The isopod tissue decreased in energy value as a result of storage (mean change -4.56%), whereas the energy value of the blueberry tissue showed no significant change following storage (mean change 0.72%).

The change in mean energy value between stored and fresh isopod tissue is more than can be tolerated for replicate pellets (Golley 1961), and in some cases may exceed the correction for endothermy (Paine 1966). This change is probably attributable to partial hydrolysis or oxidation of the highly reduced fatty acids, as neither 0_2 nor H_2O were totally excluded from the petri dishes containing the

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**1J = 0.239 cal.

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TABLE I. Energy value of some ecological material before and after storage

Material Combusted		Energy Value ± 1 SD Before Storage (J/mg-dry wt)	n	Energy Value ± 1 SD After Storage (J/mg-dry wt)	n	% Change	Method of Storage	Length of Storage	t-value	Result of t-test on Means Significance
Isopod *(Idotea baltica)*	1	15.168 ± 0.188	4	14.887 ± 0.360	4	-1.85	freeze at -15°C in covered petri dishes	9 mo	1.38	n.s.[1]
	2	12.762 ± 0.109	4	12.018 ± 0.288	4	-5.83		7 mo	10.62	p 0.005
	3	12.352 ± 0.117	4	12.005 ± 0.192	4	-2.81		7 mo	3.09	p 0.05
	4	14.419 ± 0.172	4	13.302 ± 0.218	4	-7.75		10 mo	8.05	p 0.005
Blueberry *(Vaccinium ∮ Cyanococcus)*	1	17.389 ± 0.255	8	17.623 ± 0.192	4	1.35	desiccator at 20 °C	12 mo	1.78	n.s.
	2	17.088 ± 0.222	9	16.929 ± 0.105	3	-0.93		12 mo	1.66	n.s.
	3	17.234 ± 0.322	10	17.535 ± 0.673	3	1.75		12 mo	0.75	n.s

[1] not significantly different ($p > 0.05$)

pelleted material (A. Dick, in verb.). Therefore, prolonged freeze storage of animal tissue must be considered a potential source of error in routine bomb calorimetry.

The lack of a significant change in energy content of blueberries is not surprising. Except for the seeds, blueberries are predominantly carbohydrate (Hall et al. 1971). Because carbohydrates are highly oxidized in comparison to lipids, and because free H_2O was excluded during storage, it is highly unlikely that any appreciable loss of energy would be associated with storage of blueberry tissue.

In conclusion, freeze-stored animal tissue cannot be assumed to have remained unchanged in energy content. More research, however, is required to determine the total effect of type and duration of storage on the energy content of different ecological materials.

Acknowledgements

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ERIODERMA PEDICELLATUM IN NORTH AMERICA: A CASE STUDY OF A RARE AND ENDANGERED LICHEN.*

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A single thallus of *Erioderma pedicellatum* has been found in Newfoundland near one of the 2 North American localities known thus far for this unusual lichen. Whereas almost all of the other species of the genus have tropical to subtropical affinities in their distribution and ecological adaptation, *E. pedicellatum* can tolerate winter temperatures down to near -30°C. The habitat of *E. pedicellatum* in Newfoundland has now been characterized in sufficient detail to allow the possible rediscovery of the lichen in its type locality on Campobello Island, N.B., where it was once found in association with *Erioderma mollissimum*. However, during the past 70 years, only small areas of Campobello Island have not been affected by either forest fires or logging. The fire histories in the North American localities of *E. pedicellatum* have been researched and documented, and all other obvious or possible environmental hazards to the survival of this rare and endangered lichen, including pollution and biological factors, are discussed.

Introduction

After a lapse of nearly twenty years the evasive lichen *Erioderma pedicellatum* (Hue) P.M. Jørg. has been found once again in North America. This lichen is the only exclusively boreal species of the predominantly tropical genus *Erioderma,* a member of the Pannariaceae containing the bluegreen alga *Scytonema* as a symbiont (Keuck 1977). The species occupies a rather narrow niche in some cool and highly humid parts of the boreal forest on both sides of the Atlantic Ocean. In Europe apparently all of the localities known thus far were originally discovered by Ahlner (1948) in North Trøndelag and Värmland but in spite of efforts to protect the species it has disappeared from all of these sites, the last sighting having been made in 1962 by Degelius (in schedulis). Jørgensen (1978) blamed the modern logging techniques and the deterioration of the required microclimatic conditions in the woodlands adjacent to clearcut areas for the disappearance of the species. The North American distribution is very skimpy. The type was collected by Farlow in July of 1902 on Campobello Island in New Brunswick (Jørgensen 1972), and additional material became known from the collections of Ahti made in 1956 near the base of Burin Peninsula in Newfoundland. Ahti's published *Erioderma* locality lies 13.5 km west of Swift Current near the northwestern shore of Long Pond (Ahti and Jørgensen 1971; at altitude 150 m, see loc. 25 a in Ahti 1974). It was based on several thalli collected "on thin twigs of *Abies balsamea*" (Ahti No. 9490). An as yet unpublished occurrence was communicated to me by Teuvo Ahti and is based on a single thallus collected about 3 km north-northwest of Long Pond (Ahti No. 6414, on dead fallen *Abies* in moist forest; at altitude 180-200 m, see loc. 25 b in Ahti 1974). The approximate origins of these collections have been included in figure 1 together with the newly found locality, to be described under "Ecological Observations".

In view of the established retreat of *E. pedicellatum* from Europe it became of great interest to assess the future of the species in North America.

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* NRCC No. 17764

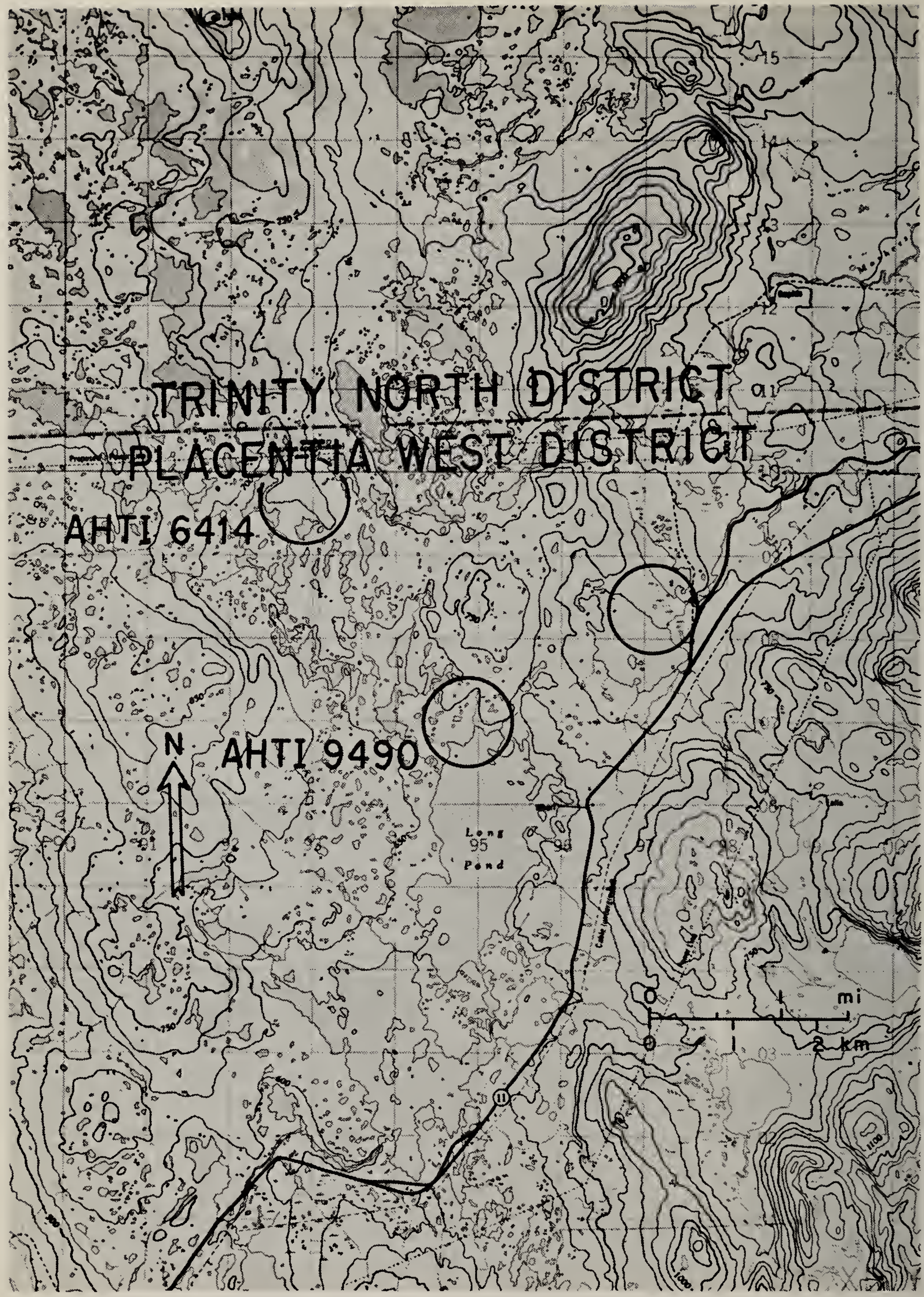


Fig. 1. Distribution of *Erioderma pedicellatum* in Newfoundland. The three localities (circled) are in close proximity to one another a little north from Long Pond and about 13 km west of Swift Current Village. The localities in which the lichen was collected by Teuvo Ahti have been placed on the map as accurately as possible by Dr. Ahti himself and are designated by his collection numbers (which do not reflect any chronological order of his collecting). The original dirt road has been straightened out and paved as inserted on the section of the map shown (reproduced from Sound Island, National Topographic Series, sheet 1 M/16, edition 2 MCE, series A 781, with permission of the Department of Energy, Mines and Resources, Ottawa). Note the great abundance of small ponds and pools in this highly humid district near the Atlantic Ocean.

Ecological Observations

During a recent exploratory trip to Newfoundland a single specimen of *E. pedicellatum* was finally located after a search for the species that had lasted several years. An old portion of the thallus has been deposited as a voucher in the Naturhistoriska Riksmuseet in Stockholm (W. Maass No. LP-18, collected 18 Sept. 1979). The remainder of the thallus has been used up for mass spectrometry, culture work and a transplant experiment to be described elsewhere.

The pocket of fir forest within which *E. pedicellatum* was discovered is seen in Figure 2. It is situated on the northeastern shore of an unnamed pond ca. 2.4 km northeast of Long Pond at 47°54′00″N and 54°21′49″W and an altitude of about 175 m (Fig. 1). The forest stand is only about 100 m wide and 300 m long, and occupies a small ridge between the lake and a bog pond surrounded by open bog. This bog showed evidence of a fire (Fig 2) which at this point must have come from an easterly direction. Within about 25 m from this affected area and behind a narrow zone of *Picea mariana* (Mill.) B.S.P. at the edge of the moat, a few of the specimens of *Abies balsamea* (L.) Mill. at the bottom of the slope showed a rich lichen vegetation closely resembling that described by Ahti and Jørgensen (1971). Several trees had *Lobaria scrobiculata* (Scop.) DC. and *Coccocarpia palmicola* (Spreng.) Arvidss. & D. Gall. on the trunks and one, with a diameter of 14 cm at breast height and rather smooth bark, contained a single thallus of *E. pedicellatum* (4.8 x 2.8 cm large) which from a

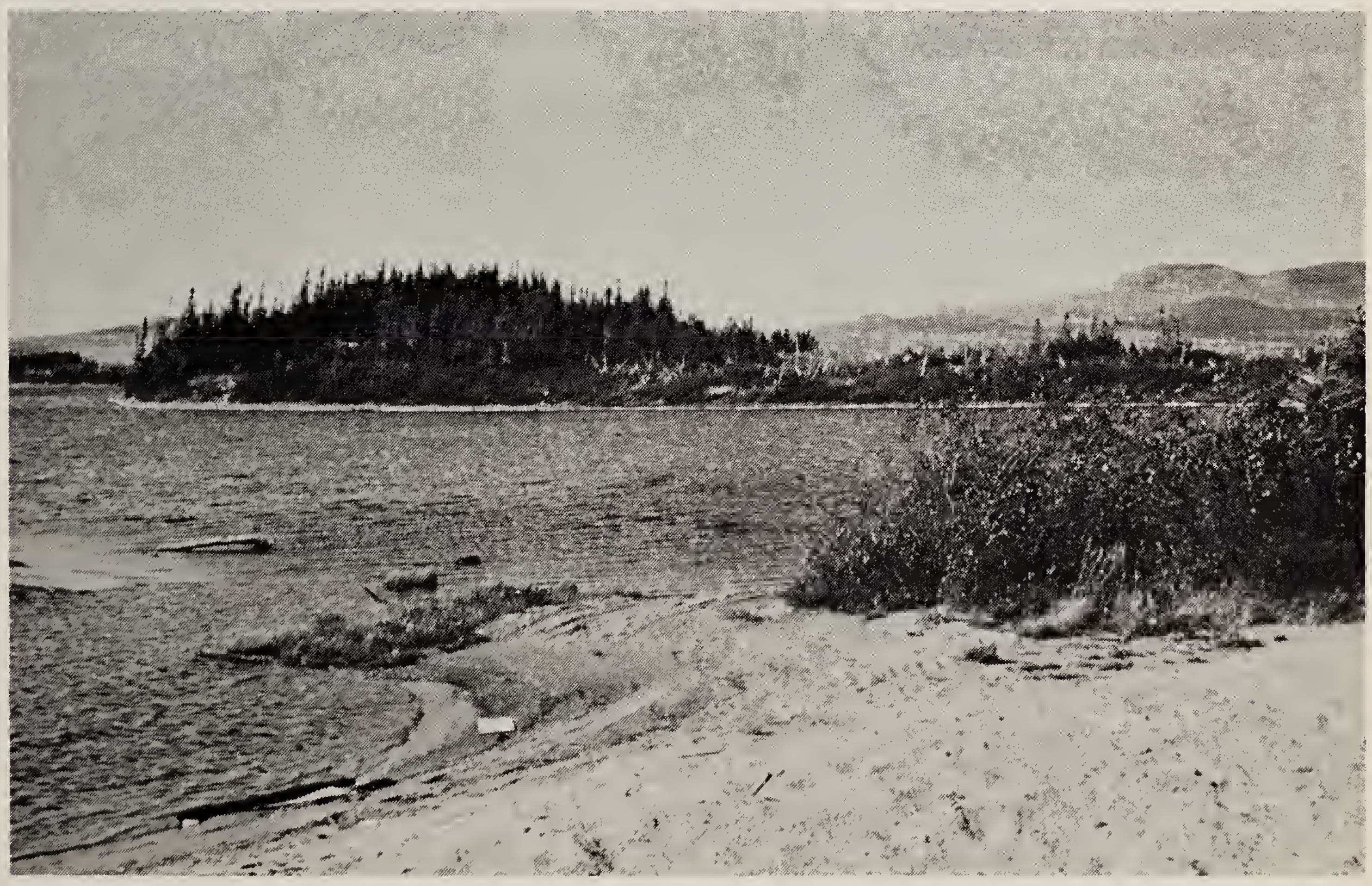


Fig 2. The locality of *Erioderma pedicellatum* 2.4 km northeast of Long Pond. The picture was taken in a north-northwesterly direction from near the southeastern corner of an unnamed pond ("Erioderma Pond") draining into the Pipers Hole River system. The pocket of mixed *Abies* forest is surrounded by a large burnt area. See text for details of the fire and habitat.

distance looked like a small version of a *Peltigera* (Fig 3). It grew on the northeastern side of the trunk at about 1.5 m from the ground (or 1.2 m as measured on the opposite side). The habitat was considerably less shaded than expected from the description by Ahti and Jørgensen. However, the lichen was moist although it had not rained for a couple of days, and in this state was dark gray to almost bluish or slate gray, which is in sharp contrast with the deep green color of the remotely related tropical species *E. physcioides* Vain. and with the grayish green color of the more closely related *E. wrightii* Tuck. The specimen displayed characteristically upturned margins showing the whitish underside with a dark hairy felt further below (Fig 4). This development of an eriostratum is much more pronounced than in material seen from Sweden and may be due to the appressed type of growth over bark. The Swedish material pictured by Keuck (1977, Fig. 204) and Ahlner (1948, Pl. 6 & 7) does not display upturned margins, which may be due to smaller thalli and their preparation as herbarium specimens. The upper side of our thallus contained the diagnostic hairs (Jørgensen 1972) and apothecia. Some of the apothecia were very

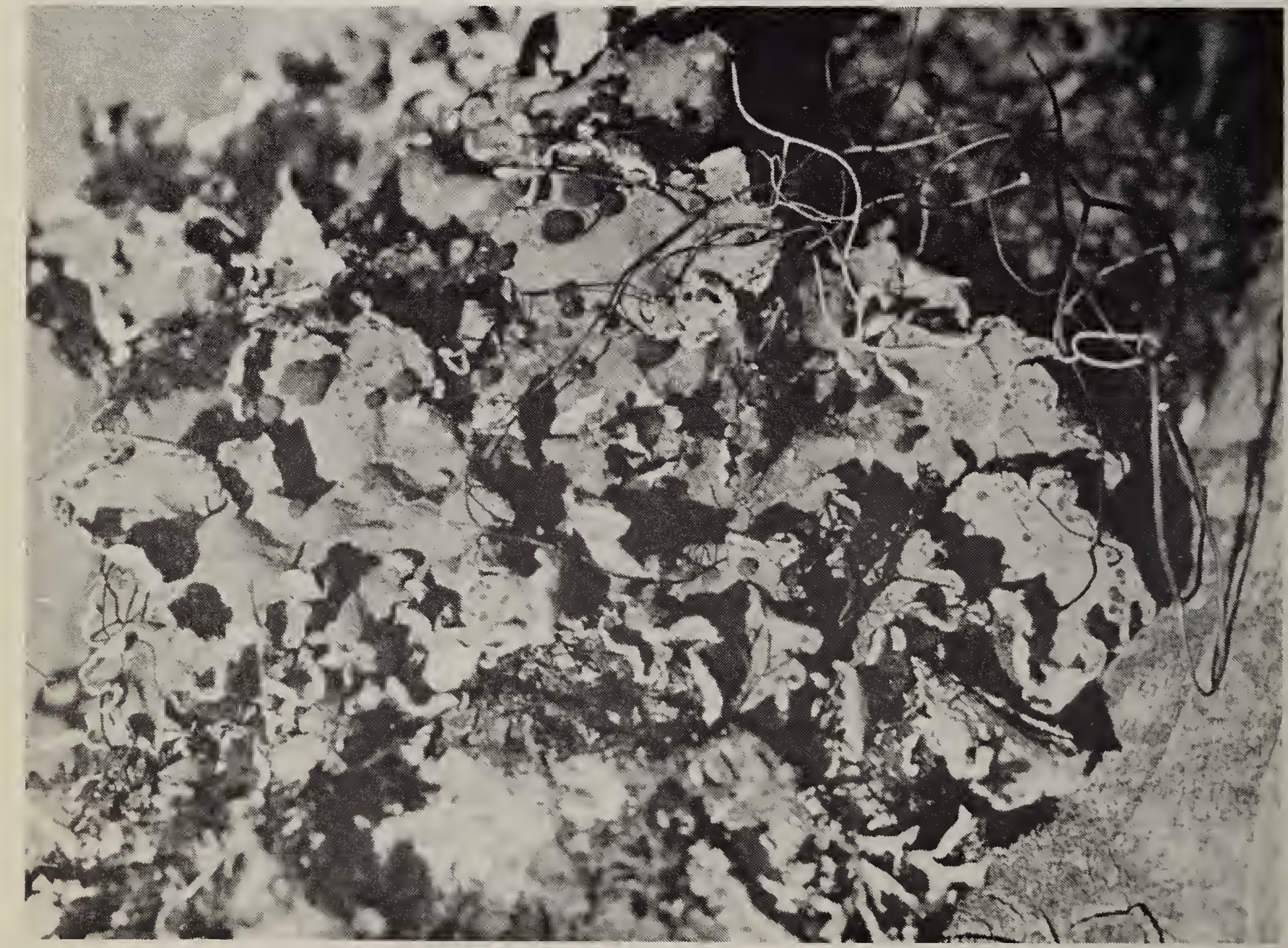


Fig 3. The thallus of *Erioderma pedicellatum* (x 2) in the moist condition. The lichen was moved into a sunny spot for the photograph. Note the upturned lobes with apothecia in all stages of development and the white marginal zone of the underside. The dark eriostratum is visible on a young lobe to the right. The old darkened portion of the thallus is at right center. The foliose *Hypogymnia vittata* and threads of the fruticose *Alectoria sarmentosa* subsp. *sarmentosa* are also seen in the picture.

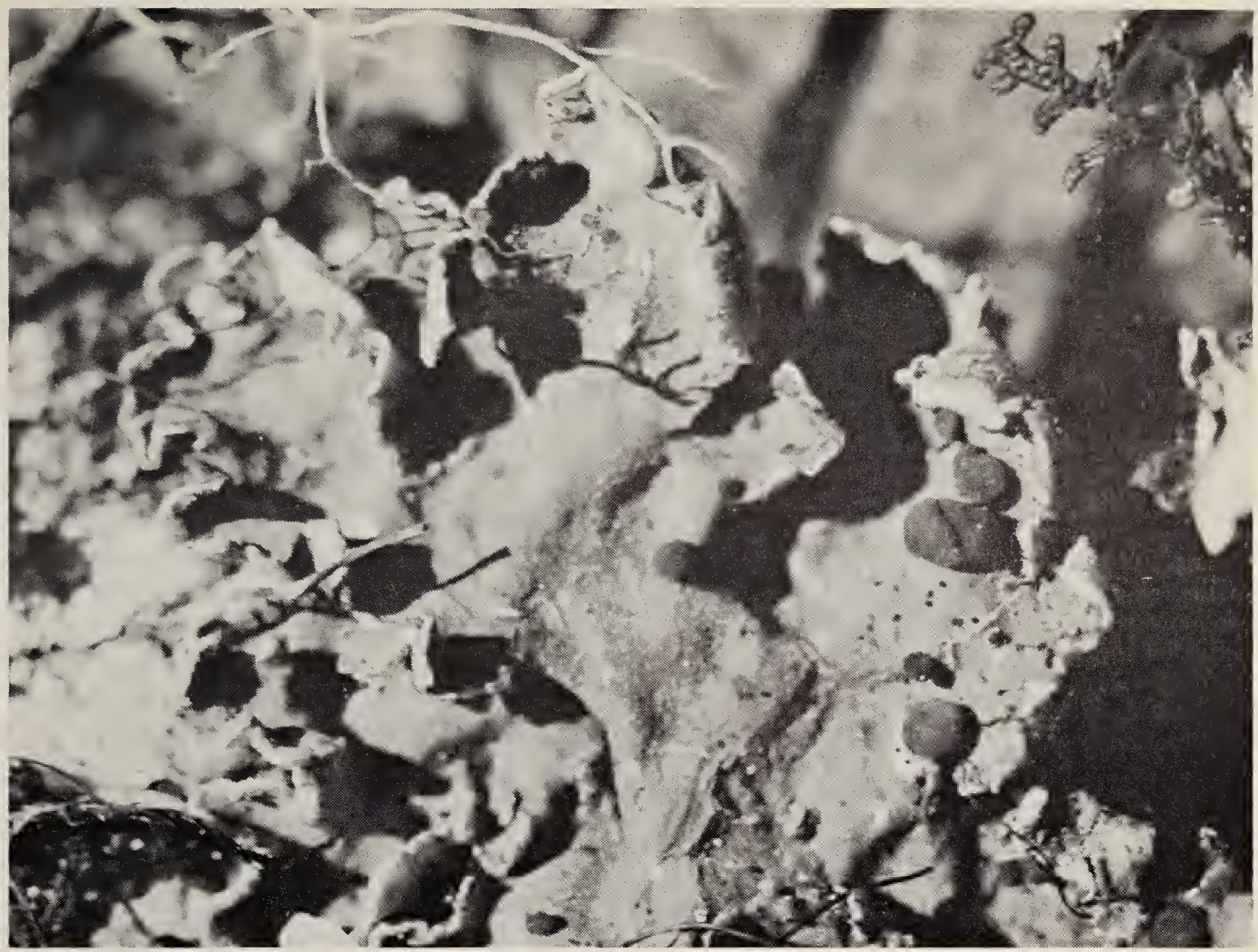
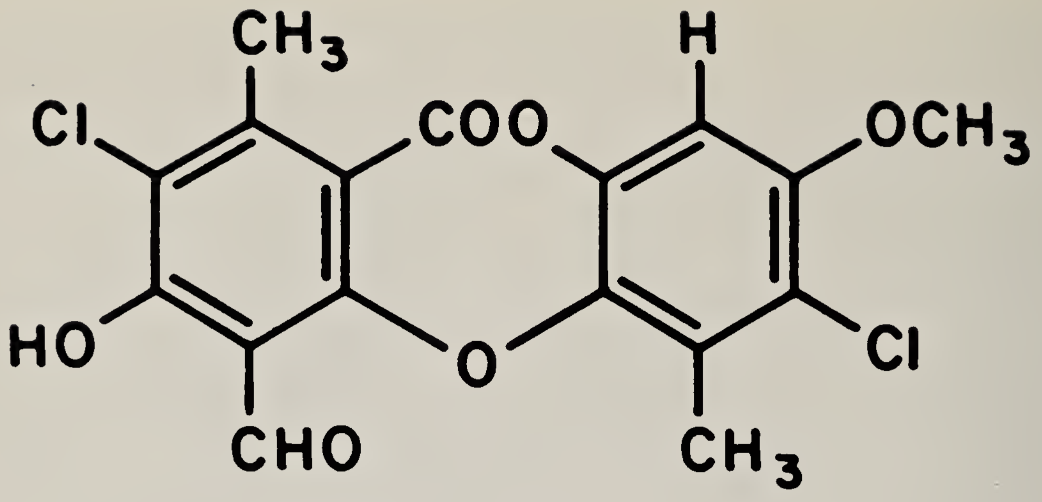


Fig 4. Close-up of *Erioderma pedicellatum* (x 4). Note the upturned margins of the lobes displaying mature apothecia, from which spores have been obtained for the cultivation of the mycobiont, and the white marginal zone of the underside followed by a dark eriostratum. *Alectoria sarmentosa* subsp. *sarmentosa* is seen near the upper edge and the hepatic *Frullania asagrayana* is in the upper right hand corner of the picture.

young and undeveloped (barely emerging from the cortex); others, however, were fully mature with a strongly convex hymenial disk, making these fruiting bodies appear semiglobose. Furthermore, the presence of a metabolite characteristic of *E. pedicellatum* (Ahti & Jørgensen 1971; Jørgensen 1972) was indicated by mass spectrometry. This metabolite is identical with the chlorinated depsidone eriodermin (Fig 5) isolated from *E. sorediatum* D. Gall. & P. M. Jørg. (Maass 1980a) and is presently known only from members of the genus *Erioderma* (Maass 1980b).

The corticolous lichens found associated with *E. pedicellatum* have been included in Table I which summarizes the available information on this unusual lichen community. On the bark of the fir tree examined, the following bryophytes were present: *Blepharostoma trichophyllum* (L.) Dum., *Frullania asagrayana* Mont., *Lophozia ventricosa* (Dicks.) Dum., *Nowellia curvifolia* (Dicks.) Mitt. and *Ptilidium pulcherrimum* (Weber) Hampe. The ground cover of the forest was mossy and made up of the hepatic *Bazzania trilobata* (L.) Gray, the mosses *Dicranum majus* Turn., *Hylocomium splendens* (Hedw.) B.S.G., *Pleurozium schreberi* (Brid.) Mitt., *Ptilium crista-castrensis* (Hedw.) De Not., *Rhytidiadelphus triquetrus* (L.) Warnst., *Sphagnum nemoreum* Scop. and *S. quinquefarium* (Braithw.) Warnst., the fern *Osmunda cinnamomea* L. and the



$C_{17}H_{12}Cl_2O_6$

Fig 5. The chemical structure of the depsidone eriodermin.

Table I. Lichens found with *Erioderma pedicellatum.*

		1	2	3
A	*Coccocarpia palmicola* (Spreng.) Arvidss. & D. Gall. [= *C. cronia* (Tuck.) Vain.]	+	+	
B	*Lobaria pulmonaria* (L.) Hoffm.			+
	L. scrobiculata (Scop.) DC.	+		+
	Nephroma bellum (Spreng.) Tuck. [as *N. laevigatum auct.*]			+
	N. laevigatum Ach. [as *N. lusitanicum* Schaer.]			(+)
	N. parile (Ach.) Ach.			+
	Pannaria ahlneri P. M. Jφrg.	(+)	(+)	(+)
	Peltigera aphthosa (L.) Willd.	+		
	P. collina (Ach.) Schrad. [as *P. scutata* (Dicks.) Duby]			(+)
	P. neopolydactyla (Gyeln.) Gyeln.	+		
	P. polydactyla (Neck.) Hoffm. s.lat. (close to *P. neckeri* Müll. Arg.)	+		
C	*Alectoria sarmentosa* (Ach.) Ach.	+	+	
	Bacidia chlorantha (Tuck.) Fink	+		
	Bryoria bicolor (Ehrh.) Brodo & D. Hawksw. [as *Alectoria bicolor* (Ehrh.) Nyl.]			+
	B. implexa (Hoffm.) Brodo & D. Hawksw. [as *Alectoria implexa* (Hoffm.) Nyl.]			+

B. nadvornikiana (Gyeln.) Brodo & D. Hawksw. [as *Alectoria altaica* (Gyeln.) Räs.]			+
B. trichodes (Michx.) Brodo & D. Hawksw. subsp. trichodes	+		
B. trichodes subsp. *trichodes,* sorediate morphotype	+		
B. trichodes subsp. *americana* (Mot.) Brodo & D. Hawksw.	+		
Cavernularia hultenii Degel.	(+)*	(+)	+
Cladonia cenotea (Ach.) Schaer.	+		
C. cf. *chlorophaea* (Flörke) Spreng.	+		
C. crispata (Ach.) Flot.	+		
C. cf. *ochrochlora* Flörke	+		
C. squamosa (Scop.) Hoffm.	+		
Graphis scripta (L.) Ach.	+		
Haematomma cismonicum Beltr.	+		
Haematomma sp. *sensu* Brodo 1968	+		
Hypogymnia physodes (L.) Nyl. [= *Parmelia physodes* (L.) Ach.]	+	+	+
H. tubulosa (Schaer.) Hav.	+		
H. vittata (Ach.) Gas. [= *Parmelia vittata* (Ach.) Nyl.]	+	+	
Lecidea albofuscescens Nyl.	+		
L. helvola (Koerb.) Th. Fr.	+		
Lopadium pezizoideum (Ach.) Koerb.	+		
Mycoblastus affinis (Schaer.) Schauer	+		
M. sanguinarius (L.) Th. Fr.	+		
Ochrolechia androgyna (Hoffm.) Arn. s.str.	+		
Parmelia squarrosa Hale [= *P. saxatilis* (L.) Ach. var. *divaricata sensu* Ahti]	+	+	
P. sulcata Tayl.	+	+	
Pertusaria sp.	+		
Platismatia glauca (L.) W. Culb. & C. Culb. [= *Cetraria glauca* (L.) Ach.]	+	+	+
P. norvegica (Lynge) W. Culb. & C. Culb.	+	+	
Protoblastenia cinnabarina (Somm.) Räs.	+		
Ramalina thrausta (Ach.) Nyl.	+		
Sphaerophorus globosus (Huds.) Vain.	+		
Thelotrema lepadinum (Ach.) Ach.		+	
Usnea longissima (L.) Ach.	+		
Usnea sp.			+

Column 1 -	Lichens on *Abies* in the newly found Newfoundland locality. Three as yet unidentified crustose species were also present.
Column 2 -	Previously reported as growing on *Abies* in Newfoundland by Ahti and Jørgensen (1971).
Column 3 -	Lichens associated with *E. pedicellatum* in Europe according to Ahlner (1948), the community being restricted here to *Picea abies* as a host tree.

+	Present.
(+)	Present in similar habitats in the same general area.
*	Found near the northeastern shore of Long Pond.

A	Cyanophilic lichen with *Scytonema*.
B	Cyanophilic lichens with *Nostoc*.
C	Lichens containing only a green alga as a phycobiont.

flowering plants *Clintonia borealis* (Ait.) Raf., *Coptis trifolia* (L.) Salisb., *Cornus canadensis* L. and *Gaultheria hispidula* (L.) Muhl. The cyanophilic lichens *Peltigera aphthosa* (L.) Willd., *P. neopolydactyla* (Gyeln.) Gyeln. and *P. polydactyla* (Neck.) Hoffm. s.lat. together with *Cladonia* species (mostly *C. crispata* (Ach.) Flot., *C.* cf. *orchrochlora* Flörke and *C. squamosa* (Scop.) Hoffm.), *Dicranum* mosses (*D. scoparium* Hedw. and *D. fuscescens* Turn.) and *Bazzania trilobata* were forming sleeves around the bases of the trunks. Some of the differences in the composition of the lichen community described from Europe (Col. 3 of Table I) and Newfoundland (Cols. 1 & 2) may well be due to the specific environment induced by the respective host tree.

It is believed that the growth of *E. pedicellatum* on a tree trunk is exceptional since previously the species was found only on rather thin twigs (either dead or alive) on the lower branches of *Picea abies* (L.) Karst. (Ahlner 1948) and *Abies balsamea* (Ahti & Jørgensen 1971; Jørgensen 1972). Our failure to detect the lichen on branches in the newly found locality is interpreted as being due to a severe reduction of the original population by the fire, the exceptional specimen on live bark being better protected from desiccation than thalli growing on twigs. That this specimen did not arrive by a more recent colonization is deduced from the extraordinarily large size of the live thallus and the fact that the latter obviously regenerated from a very old portion still recognizable but darkened and decomposed. The survival of *E. pedicellatum* in a woodlot that had been so close to the fire attests to the ability of this lichen to withstand a few days of SO_2 pollution and smoke released by the fire although the dose appears to have been deleterious. Over 11 km away, the closest village to the east which was not reached by the blaze (Swift Current) had been evacuated during this event for three days because of the massive development of smoke.

Another ecological point of interest is that *E. pedicellatum* obviously does not require a snow cover to survive the winters, as shown by the height above ground at which it was found. According to the Monthly Meteorological Summaries issued by the Department of Environment Canada, winter temperatures at the Sunnyside weather station on the isthmus of Avalon Peninsula (only about 32 km east of Long Pond at 47°51′N and 53°57′W and 46 m above sea level) fall to between -15°C and -28°C during February, the coldest month, when a snow cover may be present or absent.

The lichen community with which *E. pedicellatum* is associated throughout its range (Table I) is a variant of the "Lobarion" growing on coniferous trees. The Lobarion as it occurs on both sides of the Atlantic Ocean outside of the tropics is characterized by the presence of numerous cyanophilic lichens including some of the larger foliose epiphytes found in these regions [*Lobaria scrobiculata, L. quercizans* Michx. or *L. amplissima* (Scop.) Forss., *L. pulmonaria* (L.) Hoffm. and *Pseudocyphellaria crocata* (L.) Vain.]. The typical Lobarion occurs on hardwood trees (*Acer, Betula* and *Populus*) and is usually well developed in the mature mixed forests of eastern Canada and the adjacent United States as far as it has not been eliminated by air pollution (see Maass 1980c with respect to the change in the distribution of *Lobaria pulmonaria).* The variant on coniferous trees (*Abies, Picea, Thuja*) is especially pronounced within the fog belt of Atlantic Canada and not uncommon in the coastal areas of Newfoundland and Nova Scotia. Perhaps the limitation of this variant to cool boreal sites is related to the decreased growth rates of the conifers here, which provide a more slowly expanding bark for the establishment of lichen holdfasts.

The frequent association between *Erioderma* and *Coccocarpia,* observed in the Newfoundland localities of *E. pedicellatum* (Table I), in a habitat of *E. mollissimum*

(Samp.) Du Rietz (visited in the Great Smoky Mountains together with Per Magnus Jφrgensen in 1977), and in many tropical sites, is perhaps due to the fact that both of them contain species of the same bluegreen algal genus, *Scytonema,* as their phycobiont. For the de novo formation of thalli of *E. pedicellatum,* a species which lacks vegetative propagules but always produces an abundance of fungal spores, the presence of suitable algal cells in the environment seems necessary. In addition it is astonishing to observe that often several species of *Erioderma* occur together in the same locality (see also Jφrgensen 1972; 1979) although most of them show a very sporadic distribution pattern. This indicates the possibility that all members of *Erioderma* as well as *Coccocarpia* may employ the same species of *Scytonema* as a phycobiont. On the basis of metabolic studies discussed by Feige (1978) it seems possible that lichen algae can revert to a free-living state when the lichen association disintegrates. This would make the algae available for incorporation into new lichen thalli. As *Coccocarpia palmicola* forms isidia which function as vegetative propagules, this lichen would seem to be a possible vehicle to spread or maintain a viable population of *Scytonema* for lichenization (e.g. by *E. pedicellatum* spores). It is hoped that this hypothesis of identical phycobionts for *Erioderma* and *Coccocarpia* can be tested by the cultivation of the respective symbionts and a series of recombination experiments.

The discovery that *E. pedicellatum* can also exist under more illuminated conditions might explain the presence of the somewhat photophilous *Erioderma mollissimum* in one of the five packets of *E. pedicellatum* from Campobello Island as identified by Jφrgensen (1972). The preference of *E. pedicellatum* for cool, shaded habitats (Ahti & Jφrgensen 1971) may simply be an expression of a demand for a high relative humidity. In general, the tropical species of *Erioderma* seem to prefer steep sunlit places in the mountains above 1000 m altitude, where a high relative humidity is maintained by fairly regular afternoon rains, by dew at night and a rather dense to half-open scrub vegetation which helps to keep down the evaporation. Perhaps the only exception to this rule is our recent discovery of a presumably new species of *Erioderma** in the Blue Mountains of Jamaica which occurs in very deep shade on the mossy trunks of the elfin forest above 2000 m altitude, preferably on extremely steep slopes with eastern to northeastern exposures where winter temperatures sometimes approach the freezing point. Thus *E. pedicellatum* does not stand alone with its reported ability to live in dark forests. Moreover, the new species may turn out to be an extreme exponent of such an adaptation, as it seems to be entirely dependent on extremely low light intensities for growth.

Observations in the Type Locality

A search for *E. pedicellatum* in the type locality during repeated visits to Campobello Island has been unsuccessful. An assessment of the continued presence of *E. pedicellatum* on this island is made difficult by the fact that no precise information was given except "Campobello". Other cryptogamic collections made by Farlow in July 1902 on the island (all at FH) include *Sphagnum wulfianum* Girg. and the lichens *Alectoria sarmentosa* (Ach.) Ach. subsp. *sarmentosa, Bryoria friabilis* Brodo & D. Hawksw. on fences in association with *B. fuscescens* (Gyeln.) Brodo & D. Hawksw. var. *positiva* (Gyeln.) Brodo & D. Hawksw. and *B. trichodes* (Michx.) Brodo & D. Hawksw. subsp. *americana* (Mot.) Brodo & D. Hawksw. (see Brodo & Hawksworth 1977, who refer to the collector of these lichens as unknown; the handwriting on the labels has now been identified as belonging to Farlow), *Catillaria* sp. (on the bark of

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* to be described by Dan Nilson of the University of Göteborg.

Fagus, det. Imshaug 1951) and *Verrucaria ceuthocarpa* Wahlenb. ex Ach. A precise locality (Schooner Cove) has been given only for the *Verrucaria.* The collecting dates are not known although in Farlow's diary for July 1902 at least his visits to Bridgeport Harbor (20 July) and Middle Ground (28 July), both presumably in the U.S.A., have been mentioned. If *E. pedicellatum* was gathered near Schooner Cove, the chances are that its original habitat was destroyed by fires (Figs 6, 7). However, at least one of the more typical associates of *E. pedicellatum, Thelotrema lepadinum* (Ach.) Ach., was recently found in a *Thuja* swamp southwest of Schooner Cove (leg. W. Maass, 5 Nov. 1979, CANL). Other possible areas for the type locality are in the southern part of the island, namely between Ragged Point and Great Duck Pond (near the bog around Lost Pond), on the southeastern and northern slopes of Fox Hill (above the edges of the bogs there) and in swampy woodlands near Adam's Pond southeast of Friar Bay (Fig 7). Of these places, the only ones outside the established forest fire areas (Fig 6) and not surveyed as yet by the present author are those around Fox Hill. Perhaps here lies the hope for rediscovering both *E. pedicellatum* and *E. mollissimum,* the latter not yet having been found elsewhere in Canada or in the United States outside of the Great Smoky Mountains. In none of the locations recently studied on the island were any cyanophilic lichens seen on *Abies,* although *Lobaria scrobiculata* (very rare, near Schooner Cove and Herring Bay Head), *L. pulmonaria* (abundant only on poplar southwest of Little Whale Cove) and *L. quercizans* occasionally occur on hardwood trees. Nor was *Sphagnum wulfianum* relocated, despite a meticulous search for it. In eastern Canada this species is always found in mixed coniferous woods containing either *Abies* or *Thuja* or both, and it is quite possible that Farlow collected it in the same locality as the *Eriodermae.*

Factors Adversely Affecting the Distribution and Survival of E. pedicellatum in Newfoundland and New Brunswick

Biological factors, logging, forest fires, pollution and land development may be singled out as hazards that have been shown or are likely to affect the survival of *E. pedicellatum* in North America.

Diseases of the Host Tree and other Biological Factors

The fate of *E. pedicellatum* in Eastern North America will depend in part on the ability of its host species, the balsam fir (*Abies balsamea*), to withstand the 2-pronged attack by the spruce budworm (*Choristoneura fumiferana* Clem.) and wood-rotting fungi, most notably *Stereum sanguinolentum* (Fr.) Fr. (Basham et al. 1953). Already many of the mature stands of *Abies balsamea* have been severely decimated by these infestations. The damage along the Atlantic coast of Nova Scotia is not quite as devastating as in some of the more remote areas including parts of the Cape Breton Highlands and the isthmus connecting Nova Scotia with New Brunswick (Kettela et al. 1977). It may be assumed that this sensitivity of the host species to forest pathogens has brought about not only the deterioration of local habitats but also a change in the macrodistribution of *E. pedicellatum.*

Often in conjunction with the microclimatic habitat conditions, other biological factors such as competition by more vigorously spreading lichens and mosses as well as feeding by numerous invertebrate and vertebrate animals will also help to determine the limits within which a lichen can maintain its populations. Mites, insects (including their larvae, e.g. caterpillars) and snails may take a toll on particular lichens depending on their grazing habits and biology, even though in some cases they may contribute to the spreading of the lichen ascospores (Gerson & Seaward 1977). In the Atlantic Provinces of Canada, insects belonging to the genus *Epizeuxis*

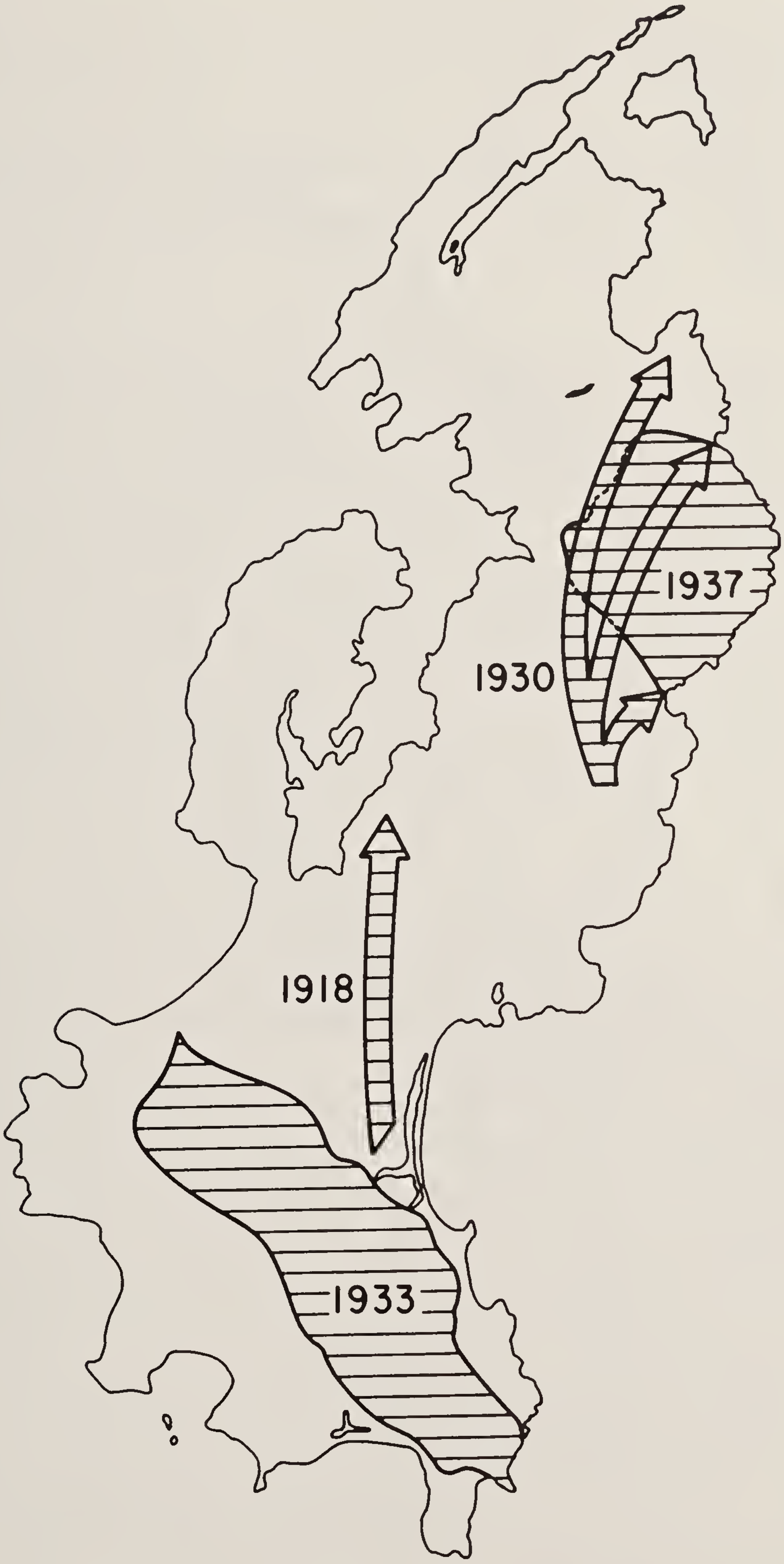

Fig 6. The larger fires on Campobello Island after 1905. The fires of 1933 and 1937 are documented by fire reports. The fire of 1918 started near the southern end of Lake Glensevern and jumped the old roads to Herring Cove and Wilson's Beach on its way to and along Harbour de Loutre. It is mentioned in a newspaper article published in the *St. John Globe* on June 6, 1918. The fire of 1930 started around May 6 near Pete's Hill and Pete's Meadow (Meadow Ice Pond), and burned through to Schooner Cove, White Rocks and Mill Cove. It was extinguished on May 10 as described in an excerpt from Deer Island dated May 12 and published in the *St. Croix Curier* of May 15, 1930.

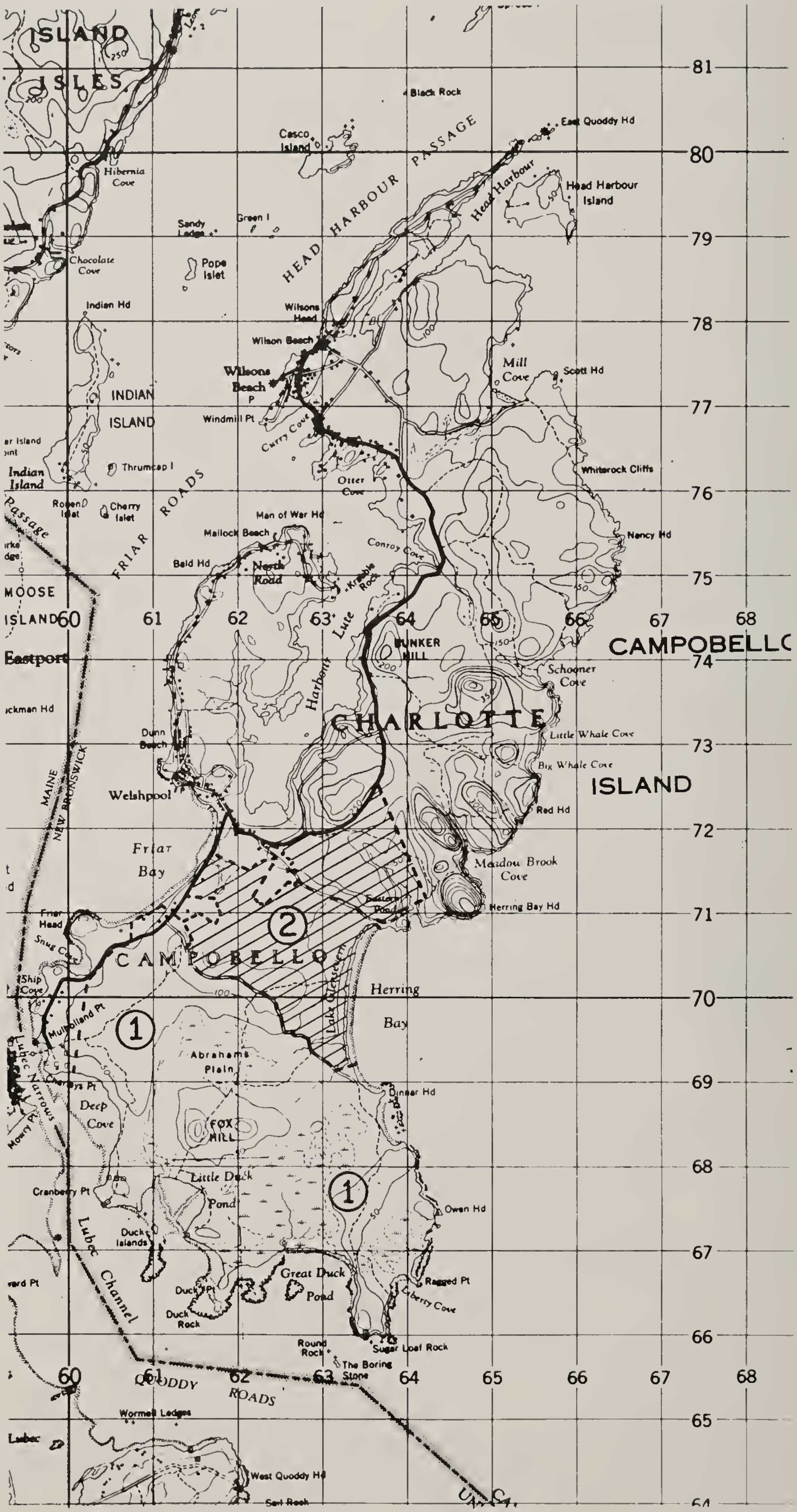

Fig 7. Topographic map of Campobello Island (reproduced from Campobello, National Topographic Series sheet 21 B/15 (west), edition 2 ASE, series A 791, with permission of the Department of Energy, Mines and Resources, Ottawa); the grid marks are 1-km^2 blocks. (1) Roosevelt Campobello International Park and Natural Area. (2) Campobello Provincial Park and Golf Lodge.

have been shown to be associated with foliose lichens on coniferous trees (Forbes 1954; Ferguson 1955). Other animals such as birds and porcupines, the latter specialized as bark eaters on coniferous trees, can damage lichens either mechanically or by their biological waste materials. Lichens in the breast-height community on the bark and twigs of fir trees may suffer also from the spring browsing of ruminant animals including moose and caribou (Peterson 1955; see also Brodo & Hawksworth 1977).

Logging

Extensive logging operations have been carried out on Campobello Island between about 1910 and 1970, first by the East Coast Lumber Company and then, after 1950, to some extent by the Dead River Company (with offices in Bangor, Me., and Fredericton, N.B.). Besides the removal of pulpwood (spruce and fir) from the land holdings of these companies (Fig 8), commercial wood has also been sold from the rest of the privately owned land, and traditionally the islanders have been cutting hardwood (birch, poplar and maple) as firewood for their own use.

Logging is also the way of life in many parts of Newfoundland although not conspicuously on or near the Burin Peninsula which largely consists of barren country. On the other hand, due to the strong winds that sometimes blow in this district, fires can become extremely serious. It may be assumed that fires have shaped the barrens which in prehistoric times must have been covered by coniferous forests surrounding all the peatlands and lakes.

Forest Fires

In the two North American stations from which *E. pedicellatum* is known, the incidence of fires has been high. The major fires on Campobello Island after 1905 have been plotted in Figure 6. It is not surprising that 1 or 2 of the large fires had started between Friar Bay and Lake Glensevern since, on this property (formerly belonging to the late Mrs. Adams), there used to be a large blueberry heath which was deliberately set afire from time to time to increase the yield of blueberries. These fires would sometimes burn out of control. Even though the exact damage from the fires of 1918 and 1930 is not on record it can be assumed that more than half of the island was struck by fire during the past 75 years. This is in sharp contrast with the mean annual burn rate of 0.13% reported by Wein and Moore (1977) for the entire southern coastal spruce-fir zone in New Brunswick within which Campobello Island lies. These authors believe that, prehistorically, this vegetation zone represents the area of lowest fire frequency in New Brunswick as it is associated with summer fog and low lightning frequency. Their data also show, however, that the more heavily populated areas in the western part of this zone are exceptional in this respect. The population of Campobello Island has been relatively constant during the past 100 years with between 1000 and 1250 inhabitants.

In Newfoundland, at least one enormous fire has swept across the area shown in Figure 1. It started on 1 Aug. 1961 near Dunn's River in the Terrenceville area and travelled in a northeasterly direction to and beyond the woodlands north of Long Pond. After reaching the Piper's Hole River Valley, the fire swung back and destroyed a significant portion of mature fir forest before it was extinguished (20 Sept. 1961). Fortunately, a few small pockets of this forest were left intact, particularly at the edges of larger bodies of water, such as on Long Pond and islands therein.

Pollution

Because *E.pedicellatum* contains a bluegreen alga as a symbiont and is thereby

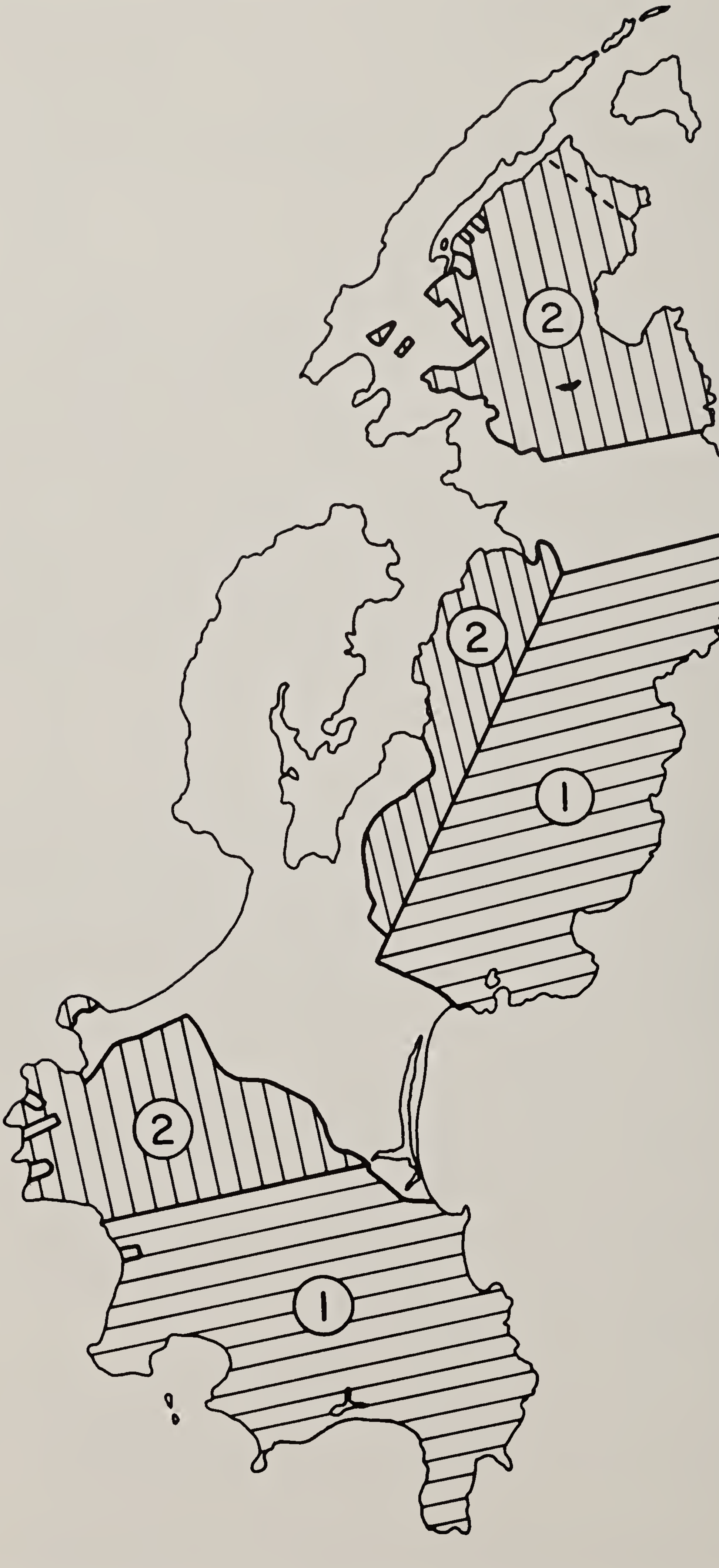

Fig 8. Campobello Island properties on which logging operations were carried out between about 1910 and 1970. Forested lands acquired by the Dead River Company soon after 1950 are shown by hatching. (1) Previously owned by the East Coast Lumber Company. (2) Previously owned by the Campobello Company.

capable of fixing atmospheric nitrogen, it may be assumed that it is highly sensitive to air pollution like other cyanophilic lichens. This predisposition is due to the inhibition of the nitrogenase activity of the phycobiont by SO_2 (Denison et al. 1976) combined with the preference of cyanophilic lichens for humid habitats. To illustrate this, none of the urban studies on air pollution and lichens that have been carried out in Halifax (Brawn & Ogden 1977), New York including Long Island (Brodo 1966), Montreal (LeBlanc & De Sloover 1970), Ottawa (Stephenson & Merriam 1975) and Winnipeg (Stringer & Stringer 1974) lists any cyanophilic lichens. In a taxonomic paper on Long Island, Brodo (1968) listed the following cyanophilic lichens as having occurred in the western half of Long Island adjacent to New York City : *Collema subfurvum* (Müll. Arg.) Degel., *Leptogium cyanescens* (Ach.) Körb., *Lobaria pulmonaria, L. quercizans, Peltigera aphthosa* var. *variolosa* (Mass.) Thoms., *P. canina* (L.) Willd. and *P. polydactyla*. However, *P. canina* was last seen in 1935 and all of the others were 19th century records (from 1866 or 1867). According to specimens at the Nova Scotia Museum of Science (NSPM) several cyanophilic lichens were collected along the Northwest Arm in Halifax in 1880 by A. H. MacKay (*Peltigera canina,* # 202; *Nephroma helveticum* Ach., # 203-B; *N. resupinatum* (L.) Ach., # 204-B; and *Leptogium cyanescens,* # 205-B) but none of these can now be found in the immediate vicinity of Halifax. Perhaps this "poliphobic"* behaviour of cyanophilic lichens can be blamed in part on the "desert effect" of cities (LeBlanc & Rao 1973), resulting in a slightly warmer and drier environment, but not in the cases of Halifax and New York where there is a strong sea climate. Similarly, in those few cases where cyanophilic lichens have been observed around mining areas (LeBlanc et al. 1974) or paper mills (Newberry 1974), they occurred only sporadically at great distances from the center of pollution (*Lobaria pulmonaria* 20 km and *L. quercizans* 13 km away, respectively). Cyanophiles are also suspected to be sensitive towards other types of pollution, since they were absent from an area of about 250 km^2 around the aluminum smelter at Arvida, Que., which emits hydrogen fluoride pollution (LeBlanc et al. 1972), and since Nash (1975) failed to report their presence in the mountainous woodlands near the zinc factory at Palmerston, Penn. Wielgolaski (1975) even reported on some experimental evidence according to which the cyanophilic lichens may be strongly reduced in those rural areas which suffer from strong, mostly global pollution, such as in southern Norway. In good agreement with this are the observations by Jφrgensen (1978) on a general decline of members of Pannariaceae in Västergötland, Sweden, although changes of habitat conditions due to the partial removal of forests have been shown by him to be also very important. For these reasons it is not improbable that *E. pedicellatum* has already suffered from a similar deterioration of the air quality in North America.

Little is known of the chemical effect of the spraying of the woodlands against the spruce budworm upon the populations of lichens on balsam firs. In some forests of southern New Brunswick that have been treated with aerosol sprays containing pesticides a spotty discoloration of the foliose macrolichens can be observed. The harmful agents may be the pesticides themselves or the emulsifiers used for their dispersal in tiny droplets. The following pesticides have been applied to the forests of New Brunswick on a large scale: DDT (between 1952 and 1968), fenitrothion (from 1968 until now) and (in 1979) aminocarb (Matacil). On a more or less experimental scale, phosphamidone, carbaryl (Sevin) and *Bacillus thuringiensis* (BT) have also been tried. In Nova Scotia only BT has been used, in Cumberland County and the Cape Breton Highlands in 1979. Newfoundland has seen the application of pesticides in 2 spray programs; one was directed against the hemlock looper (*Lambdina fiscellaria* Gn. f. *fiscellaria* Gn.) and employed fenitrothion (between 1968 and 1972), and a more recent one against the spruce budworm. In connection with the latter, the following compounds were tried in 1977 over a total of about 81,000 ha: fenitrothion, Matacil, acephate (Orthene) and BT. The following year saw the application of only Matacil over almost 810,000 ha, and in 1979 6000 ha were sprayed with BT. The relevance of these spray programs for the survival of *E. pedicellatum* is the possibility that this lichen is sensitive to some of the sprays and the fact that one of the sprayed areas (Bonavista Peninsula) was less than 65 km away from Long Pond. Sprays delivered from planes may be carried as far as that by winds. A general study of the effect of these biological control agents upon tree-dwelling lichens and their symbionts is needed, not only to establish any possible ranking in their sensitivities but also to investigate the potential of lichens in the biological degradation or inactivation of these pesticides which are often unpredictably harmful to both animals and man. So far, only the breakdown of a chlorinated biphenyl derivative has been investigated in lichens (Maass et al. 1976), and numerous parallel studies of the metabolism of this simple model of an industrial pollutant have shown that the pathways for the biological breakdown of this and similar compounds are probably no different in lichens than in other organisms. No information exists on the effect of BT upon lichens although much work has been carried out on the possible side effects of this bacterium in other living systems. In particular BT has been shown to have chitinolytic activity (Smirnoff & Valero 1977). This property of BT could result in the degradation of the cell walls of the mycobiont or at least interfere with its chitin metabolism. Such events might in turn upset the precarious balance of the symbionts and destroy the integrity of the lichen.

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*Derived from the Greek words πόλis (polis = city) and ϕoβós (phobos = avoidance).

Land Development

Land development has not as yet been significant in the areas under discussion except for the building of roads and power lines and, on Campobello Island, the establishment of a golf course, campground, and a gravel field operation. In fact, the conversion of the southern part of Campobello Island into parks ("Roosevelt Campobello International Park and Natural Area" and "Campobello Provincial Park", Fig. 7) will protect these lands from commercial over-exploitation. However, the forested and rugged eastern coastal strip outside of these parklands is not presently being conserved although it is among the most spectacular in the Maritimes. According to a development plan of 1970 made for the Dead River Company it has been designated for possible future cottage lot development and a study of its lichen flora is a matter of urgency.

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Maps in Figures 1 and 7 Her Majesty the Queen in Right of Canada, 1971 and 1954 respectively. Reproduced from maps of the National Topographic System with permission of the Department of Energy, Mines and Resources, Ottawa.

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NITROGEN FIXATION (C_2H_2 REDUCTION) BY LUNGWORT LICHEN (LOBARIA PULMONARIA **(L.) HOFFM.)** ON RED MAPLE (ACER RUBRUM **L.**)

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A study of nitrogen fixation using the acetylene reduction technique by the lungwort lichen was carried out to investigate the nitrogen inputs of a forest stand. The lichen grew predominantly on red maple, occurring on 23% of the stems and reaching the highest coverage on trees of DBH 20 to 25 cm. Total coverage of the lichen was 12.7 m^2 ha^{-1}.

Forty-seven acetylene reduction assays indicated that N_2 fixation rates were very variable principally as a result of variation in thallus moisture. Cumulative N_2 fixation for each month was estimated from precipitation, temperature, and day length data. Stemflow was also collected and samples from above and below the lichen were compared.

Soils in the study area had only 2 kg ha^{-1} of nitrate so even small inputs are important. However, the total input from lungwort was calculated to be only 3.5 gN ha^{-1}. The maximum rate estimated for a single tree would be equivalent to about 5% of the annual nitrogen requirements of the canopy foliage. Although these rates are about three times those of others reported in the literature, they are not believed to be very important.

The stemflow studies also indicated that this input was small, and decomposition of the lichen thallus would yield less than 1% of the nitrogen present in red maple leaf litter.

Introduction

The nitrate levels of soils in most Halifax County forests are extremely low. Nitrate levels of 2 kg per hectare were reported by the Nova Scotia Department of Agriculture for samples from the study site in the Waverley Game Sanctuary.Such low concentrations of this nutrient may limit productivity in this area. Therefore, it is important to reveal the sources of nitrogen that operate in these forest ecosystems.

Nitrogen fixation by living organisms is an important source of reduced nitrogen in ecosystems (Kelly & Becker 1975). The process involves the reduction of atmospheric nitrogen to ammonia which is catalyzed by nitrogenase. Only prokaryotic organisms are capable of fixing dinitrogen and they are found in a variety of associations in the forest.

A preliminary survey of forest sites in the Waverley Game Sanctuary indicated that the nitrogen fixing lungwort (*Lobaria pulmonaria* (L.) Hoffm. **) appeared only to occur on *Acer rubrum* stems. The objective of this study was to estimate the quantity of nitrogen fixed by lungwort, assess its possible significance as a nitrogen input to the forest ecosystem, and investigate the implications of lungwort's occurrence on *Acer rubrum*.

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**Hereafter referred to as lungwort in this paper.

Literature Review

Biology of the Lichen

Lungwort is a foliaceous, corticolous lichen of the *Stictaceae*. The thallus is comprised of a lichenized ascomycete mycobiont with a chlorophycean and a cyanophycean phycobiont. The chlorophycean component has been determined as *Myrmecia* (Ahmadjian 1969), which forms a continuous layer throughout the thallus and the cyanophycean is *Nostoc*. The blue-green alga is arranged in compressed clusters in internal cephalodia (Jordan 1970). Lungwort produces both soredia and isidia, usually along the thickened portion of thallus, which make it easily recognized. This species is the most widely distributed and most commonly collected *Lobaria* in North America (Jordan 1973).

Nitrogen Fixation by Lichens

Lichens which possess a blue-green alga as a thallus component have the ability to fix atmospheric nitrogen (Millbank & Kershaw 1969; Henriksson & Simu 1971; Hitch & Stewart 1973). About 50 species have demonstrated this capability. Studies by Millbank and Kershaw (1970) first indicated that lungwort was such a species, and that fixation was limited to the internal cephalodia, implicating *Nostoc* as the fixing phycobiont.

Dinitrogen heavy isotope investigations by Millbank and Kershaw (1970) on *Peltigera aphthosa* indicated that the labelled nitrogen fixed by *Nostoc* in the cephalodia had been transferred to and was overwhelmingly present in the mycobiont. Virtually all of the nitrogenous compounds produced by *Nostoc* are translocated to the mycobiont, which could be of vital significance to the maintenance of healthy growth of the thallus (Millbank & Kershaw 1970).

Nitrogen fixation is highly dependent on the metabolism of the lichen, thus environmental conditions that affect the metabolic rate are reflected in the rate of nitrogen fixation (Millbank & Kershaw 1973). Lichens are opportunists; metabolism is highly variable and depends largely on the thallus water content and temperature. Thus when conditions are suitable for assimilation and synthesis, the processes become active and when conditions deteriorate they revert to a state of quiescence (Millbank & Kershaw 1973).

The most important environmental factor affecting nitrogenase activity is the thallus moisture content (Hitch & Stewart 1973; Kershaw 1974). Henriksson and Simu (1971) reported the ability of *Peltigera* to recover its nitrogenase activity after prolonged periods of desiccation. The recovery rate is rapid after short drought periods, but recovery takes progressively longer as the drought period is extended (Kershaw & Dzikowski 1977). Kershaw (1974) found that each of the 12 species of lichen used in his study had different patterns of fixation response to changing levels of thallus moisture. These patterns were correlated with the ecological preferences of each species.

Another significant environmental factor concerning nitrogenase activity is temperature (Millbank & Kershaw 1969; Hitch 1971). Maikawa and Kershaw (1976) studied the temperature dependance of nitrogenase activity in *Peltigera canina*. They found that the optimum temperature varied seasonally with ambient temperatures. Subsequent work by Kershaw (1977) showed that lichens are able to photosynthetically acclimatize to lower temperatures. Considering the relationship between rates of metabolism and N_2 fixation, this may explain the seasonal changes in optimal fixation temperatures. Kelly and Becker (1975) indicated an optimum fixation temperature of 30°C for lungwort samples collected in North Carolina. No activity was detected at 10°C. The seasonal variation in activity with temperature was not studied, and water-saturated samples were incubated at various temperatures without acclimatization periods.

The final major nitrogenase parameter is the level of light intensity (Kallio et al. 1972; Kallio 1973). Stewart (1965) showed that *Nostoc* was capable of some dark N_2 fixation, but it was considerably less than in light. MacFarlane et al. (1976) examined the interaction of light/dark periods in relation to the nitrogenase activity in *Peltigera polydactyla,* and calculated there was an immediate 50% decrease in activity when the lichen was darkened. There was a progressive further decrease with time. Results indicated a lag phase in activity upon re-illumination before it recovered to its original level.

The influence of light intensity on nitrogenase activity in lungwort was tested by Kelly and Becker (1975). Activity was shown to increase when the lichen was exposed to light intensities in excess of typical values found in shaded forests. Light saturation was never observed in the tests and is presumed to be above the maximum intensity used in the study (1200 Einsteins m^{-2} sec^{-1}). Kelly and Becker attributed the high saturation for lungwort to the embedded cephalodia.

Lichens as a Nitrogen Source

Nitrogen-fixing lichens have been shown to be important nitrogen contributors to their surroundings, especially in arctic and sub-arctic regions where they are the primary source of reduced nitrogen (Alexander & Schell 1973). Denison (1973) estimated that *Lobaria oregana* on tall Douglas fir contributes from 2.2 to 11.2 kg $ha^{-1}yr^{-1}$ to the forest. Becker et al. (1977) calculated a total nitrogen input of 1.23 g $ha^{-1}yr^{-1}$ for all nitrogen fixing corticolous lichens in a North Carolina oak-hickory forest.

According to Denison, nitrogen fixed by the lichen is released in several ways to the forest. The chief route of contribution is through decomposition processes such as bits of old thallus breaking off. Most of this removal is caused by the peeling action of rain, snow, and ice. The rapid nitrogenase rate probably enables more nitrogen to be fixed than the lichen can utilize for new growth (Denison 1973). This soluble excess of nitrogenous compounds may be leached with other metabolites from the thallus after rewetting owing to increased permeability and structural damage to cell membranes during desiccation (Farrar 1973; Crittenden & Kershaw 1978). Thus nitrogen may be washed down the tree by precipitation.

Stemflow

The proportion of rainfall intercepted by trees can be divided into 3 components: tree surface absorption, drips from leaves and branches (throughfall), and water flow down the trunk (stemflow). The relative proportion of the 3 components of interception depends on the quantity and duration of precipitation and the forest structure. The percentage of intercepted precipitation which reaches the ground surface as stemflow varies with tree species and is related to bark characteristics and the angle of branching. Rainwater becomes enriched in certain elements derived from trees (Kittredge 1948; Will 1955; Voigt 1960). It is well documented in the literature that losses of some elements from above-ground plant parts may occur by leaching (Tamm 1951). Gersper and Holowachuk (1971) produced evidence that the initial flush of stemflow has a higher concentration of elements than any subsequent flow during the same rainstorm. They attribute this to washing of particulate matter from the foliage and stems by the initial precipitation.

The quantitative contributions of stemflow to the nutrient cycle are small (Voigt

1960; Mahendrappa 1974). Voigt (1960) observed differences in stemflow distribution under different tree species and found the influence of stemflow was limited to a small distance (about 30 cm) from the tree stem. Zinke (1962) and Gersper and Holowachuk (1971) have also concluded that quantitative variations in the physio-chemical properties of soils near the trees have been caused by stemflow.

Mahendrappa (1974) studied the chemical composition of stemflow from some eastern Canadian tree species. His results indicated that stemflow of *Acer rubrum* had a higher pH (4.8) than stemflow of *Picea resinosa, Abies balsamea,* and *Pinus strobus.* His work is in agreement with Tamm (1951) and Voigt (1960) in indicating that rain seemed to leach more nitrogen from hardwoods than from softwoods. The estimated annual quantity of nitrogen returned to the ground by stemflow from *Acer rubrum* was 0.066 g stem^{-1}. The trees in this 55-year-old stand had an average height and DBH* of 16.8 m and 23 cm respectively.

Ecology of Corticolous Lichens

In forested regions, lichen communities form a complex mosaic that is broadly correlated with forest composition and tree density (Kershaw 1964). There are many factors implicated in determining the distribution of corticolous lichens within forests. The availability of water and a suitable substrate are the chief considerations (Barkman 1958). Hale (1955) concluded from a study of contiguous woodlots that about 60% of the variation in lichen communities could be caused by substrate factors and 40% by microclimate.

Lichens are termed poikilohydric as they passively follow the fluctuations of atmospheric humidity. Lichens do not have specific organs for the absorption or transpiration of water. Absorption of water into the hyphal walls occurs rapidly. Full saturation can be achieved in 1 to 4 minutes for foliose thalli immersed in water (Smith 1961). Water is easily lost by evaporation from the thallus surface. Field observations have shown that saturated thalli dry out within a few hours in dry weather (Blum 1973).

Foliose lichens possess the ability to absorb water vapor from the atmosphere (Pavillard 1939); however, it requires several days to equilibrate and only 50 to 75% of the potential levels of saturation can be obtained. The maximal saturated water content of lichens under natural conditions is achieved only during rain showers and for short periods thereafter (Blum 1973). Atmospheric humidity, however, is an important factor influencing water loss through evaporation (Barkman 1958). Relative humidity is known to vary with forest density, and with proximity to the forest floor.

The drought resistance of the genus *Lobaria* was examined by Lange (1953). The thalli endured 24 weeks in a desiccator without signs of visible damage.

The role of the bark supporting lichen thalli is complex. "It is open to question whether lichens derive any nutriment from their support at all" (Brodo 1973). It is clear that lichens have substrate preferences. The extent to which a lichen is restricted to a narrowly defined substrate type can be called its substrate specificity (Barkman 1958). The most important bark properties that govern lichen occurrence are texture, water relations, chemistry, and stability.

The texture of bark affects the ease of colonization. Lichen diaspores can become trapped and begin to develop on rough surfaces more easily than on smooth surfaces (Brodo 1973).

Differences in lichen floras have been attributed to bark-water capacities (Hale 1955; Culberson 1955; Margot 1965). Harris (1971) found that substrate moisture acts

*diameter at breast height (1.3 m)

in the hydration of the thalli, thereby influencing the lichens' rate of photosynthesis and respiration. Lungwort has been reported to favor *Quercus* in coastal regions but *Fagus* in inland areas because of the high water capacity of *Fagus* bark (Barkman 1958). This supports the theory that lichens respond to bark characters, not to tree species. In analyzing epiphytic vegetation on *Acer* and *Pinus,* des Abbayes (cited by Brodo 1973) concluded that *Acer* did not only retain more moisture than did *Pinus,* but liberated it more regularly and made it available to lichens over a longer period of time and at higher levels.

Of all aspects of substrate chemistry which might be considered, pH has been the most studied and discussed. The acidity or alkalinity of the substrate can act indirectly on lichen thalli in numerous ways. The "availability" of various minerals and organic substances varies under different pH regimes. Diffusion rates may change at different pH's, and some substances are more toxic under acidic conditions (Brodo 1973). A direct influence of pH might operate through the effects on the activity of enzyme systems in the lichen (Brodo 1973). Whatever the mechanism of influence, studies by Culberson (1955) and Kershaw (1964) have demonstrated that the distribution of some lichens and lichen communities is strongly correlated with substrate acidity. The presence of lichens on a tree trunk modifies the pH (Kershaw 1964). Uncolonized areas have lower pH's than those that are colonized. Conifers generally have a lower pH than hardwoods. In particular, the buffering capacity of bark is important.

The final substrate parameter considered is the stability of the bark. Since lichens are slow growing, they are generally more abundant on trees whose bark is seldom sloughed (Becker et al. 1977).

Most of the bark substrate qualities (texture, water relations, chemistry, and stability) vary with the vertical distribution on the tree stem. The bark texture generally becomes coarser at the base of the trunk. Studies by Kershaw and Harris (1971) indicated that the vertical distribution of *Parmelia* on tree trunks was determined by water availability. The pH also varies at different levels on the tree stem, the upper layers having a higher pH than the lower (Kershaw 1964).

Competitive interactions occur among epiphytic lichens. Competition may be categorized as suffocation, competition for light, and chemical action (Barkman 1958). The chief competitors at the lower trunk levels are bryophytes. Bryophytes growing in dense mats sometimes overgrow lichens (Hale 1967). Epiphytes belonging to higher strata tend to crowd out those of lower strata by over-shadowing them (Barkman 1958).

Generally, as the tree and branches grow and the crown and canopy of the forest develop, the lower parts of the tree are shaded and lichens become distributed along the trunk in response to their environmental needs. As a result, a characteristic vertical pattern is produced (Kershaw 1964).

Description of the Study Area

All field work for this study was conducted in the Waverley Game Sanctuary along a 3-km section of the Old Guysborough Road. The Sanctuary is situated 20 km northeast of Halifax and comprises 52.3 km^2 of crown and privately owned land.

The underlying rock in the study area is quartzite of the Gold-bearing Series. The thin layer of soil covering the rocks is categorized as steepland till. The soil has a sandy-clay-loam texture with coarse, stony fragments. Soil analysis by the Nova Scotia Department of Agriculture indicated that the soil is moist, acidic (pH 3.4), and about 45% organic matter.

The area is covered by a second-growth forest of moderate density (Lewis 1963). In the study area, the most frequent tree species were *Picea rubens, Abies balsamea,* and *Acer rubrum,* with occasional occurrences of *Pinus strobus, Betula papyrifera,* and *Picea mariana.*

Materials and Methods

Ecology of Lungwort

Ten 400-m^2 quadrats were randomly chosen at least 30 m from the Old Guysborough Road.

Preliminary observations indicated that lungwort occurred predominantly on *Acer rubrum* in this locality. To substantiate this observation, stems on each plot were systematically examined and a census of all *Acer rubrum* stems with a DBH greater than 5 cm was conducted. If the lichen occurred on a stem, the tree species was noted and its DBH measured to give an approximate estimate of age. The vertical distribution was also recorded. To make a quantitative estimate of lungwort coverage, at least 8 randomly chosen trees on each plot (where available), were tested for percent cover using the cover pin technique (Goldsmith & Harrison 1976). Since lungwort thalli tend to overlap, and the cover pin technique only quantified in 2 dimensions, a correction factor was calculated from the frequency of the cover pin hitting areas of thallus overlap. Because of height limitations, the percent cover determined by this method applied only to the lower 2 m of the stem. Above this height, the coverage was estimated by visual inspection.

To determine whether the alteration in microclimate resulting from *Acer rubrum* stump sprouting affected lungwort coverage (per stem), the number of stump sprouts was recorded (Prager & Goldsmith 1977).

Nitrogenase Activity of Lungwort

The nitrogenase activity of the lungwort was measured in the field using the acetylene reduction technique (Hardy et al. 1973). Nitrogenase catalyzes the conversion of acetylene to ethylene and thus the quantity of ethylene provides a direct measure of nitrogenase activity. A 3.2:1 molar ratio of ethylene produced to nitrogen fixed was used to estimate N_2 fixation (Hardy et al. 1973).

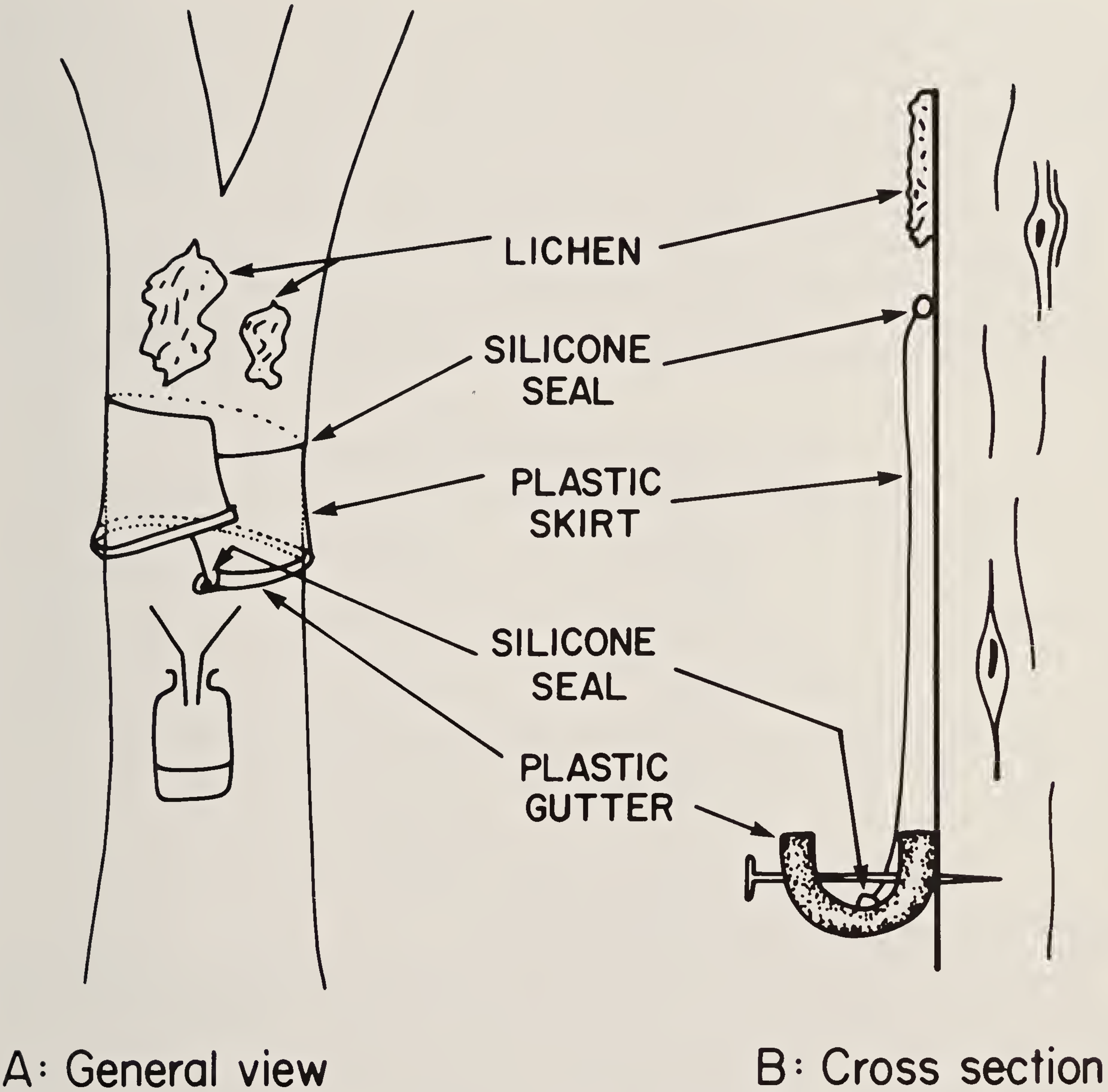
Portions of intact lungwort mats were removed from stems and placed in 1000-ml Mason jars with a serum cap embedded in the lid. The appropriate amount of acetylene was injected to produce a 10% atmosphere of this gas. The incubation jars were then placed on the forest floor at the collection site.

Gas samples were taken in evacuated blood-sampling tubes. An initial ethylene reading was taken 5 min after acetylene injection. Data from time course experiments indicated that a l-h incubation period was sufficient to estimate ethylene production. After the gas samples were collected, the lungwort was transported to the laboratory where the thallus surface area, fresh weight, and oven dry weight (24 h at 90°C) were determined.

Gas samples were analyzed by gas chromatography on a Carle Model 9500 flame ionization gas chromatograph, equipped with a 0.32 x 50 cm, 80/100 mesh Poropak T column. Nitrogenase activity was measured in the months of April, May, June, September, and October of 1978 and February of 1979.

Stemflow Collection

To measure the amount of nitrogen that may be added to stemflow as it passes



A: General view

B: Cross section

Fig. 1. Apparatus for collection of stemflow from *Acer rubrum* trunks. Another plastic skirt was fastened over the area of lungwort colonization to collect samples that had not run over the lichen.

over the trunk, and determine the possible contribution by lungwort, throughfall and stemflow samples were collected and analysed for nitrogen content.

The apparatus used to collect stemflow consisted of a gutter formed by a split 1.5-in d plastic tubing fastened around the circumference of the trunk. A funnel with a 1/16 in and a 100 μm filter screen was attached to the lower end of the gutter. The funnel was 7-cm d so very little throughfall was collected (10%). An acid-washed 250-ml plastic collection bottle was taped securely to the funnel. Above this assembly, a polyethylene skirt was adhered to the stem and gutter with silicone (Fig 1). Another longer skirt (about 0.6 m), could be placed over the lungwort to prevent stemflow from passing over lichen thalli. Two such devices were constructed on *Acer rubrum* stems where lungwort only occurred as high percentage cover band on the trunk.

Throughfall was collected in troughs made from 3-m sections of split, 5-in d PVC pipe. The trough channeled throughfall to the same type of filters and collection container used for stemflow.

Stemflow samples that had passed over lungwort and those that were prevented from doing so, were collected on the same tree from the same rainstorm. Throughfall samples were also collected at this time. Collection was made during each rainstorm. Samples were placed immediately in a cooler and frozen within 3 h of collection. The samples were stored at -3°C until they were analysed for nitrogen.

The Kjeldahl technique (Bremner 1965) was used to determine the total reduced nitrogen concentration in duplicate 50-ml aliquots from each collection.

For calculations, the volume of stemflow for *Acer rubrum* was taken to be 5.6% of total rainfall (Mahendrappa 1974). The average canopy cover for this species in the study area was estimated at 7.4 m^2. Annual nitrogen requirements for *Acer rubrum* (Table I) were calculated from data of Young and Carpenter (1967).

Table I. Mean annual nitrogen requirements for a 30-35′ *Acer rubrum*

Foliage	2.0 gN
Branches	1.3 gN
Stems	4.6 gN
Roots	1.9 gN
Total	9.8 gN

Estimation of Annual Quantity of Nitrogen Fixed

Estimation of annual nitrogen fixation by lungwort was calculated by combining environmental parameters governing nitrogenase activity, determined from both this study and from the literature, with meteorological data compiled by Environment Canada (1978). The calculation considers lichen-water relations (wetting and drying rates) and monthly variations in daylight hours and temperature.

To estimate the moisture content of the thallus for a given rainfall, data produced by Harris (1972) were used. His results indicate that an average of 5.3 mm of rain is necessary to saturate the bottom 2 m of corticolous lichen situated on a deciduous tree during the winter when no canopy is present; 8.3 mm of rain is necessary when the canopy is present. These values were used in the calculation, and after each rainfall in the calendar year 1978, lungwort thalli were assumed to be saturated. The period of canopy cover was designated from May to October.

The drying rates for lungwort were obtained from a linear regression calculated from values of lichen percent moisture after various periods of desiccation following saturating rain events (Fig 2).

Seasonal variation may be expected in evaporation rates. In winter months low temperatures would decrease rates. However, the loss of full canopy increases wind velocities within the forest thereby increasing evaporation rates. In these calculations, the same evaporation rates were used for all seasons. The nitrogenase activity rate for each day following saturation was determined from the ethylene-production-moisture graph (Fig 3).

It was assumed that N_2 production is restricted to daylight hours. To account for the seasonal variations in day length at 45°N latitude, median values for each month as provided by Environment Canada (1978) were used.

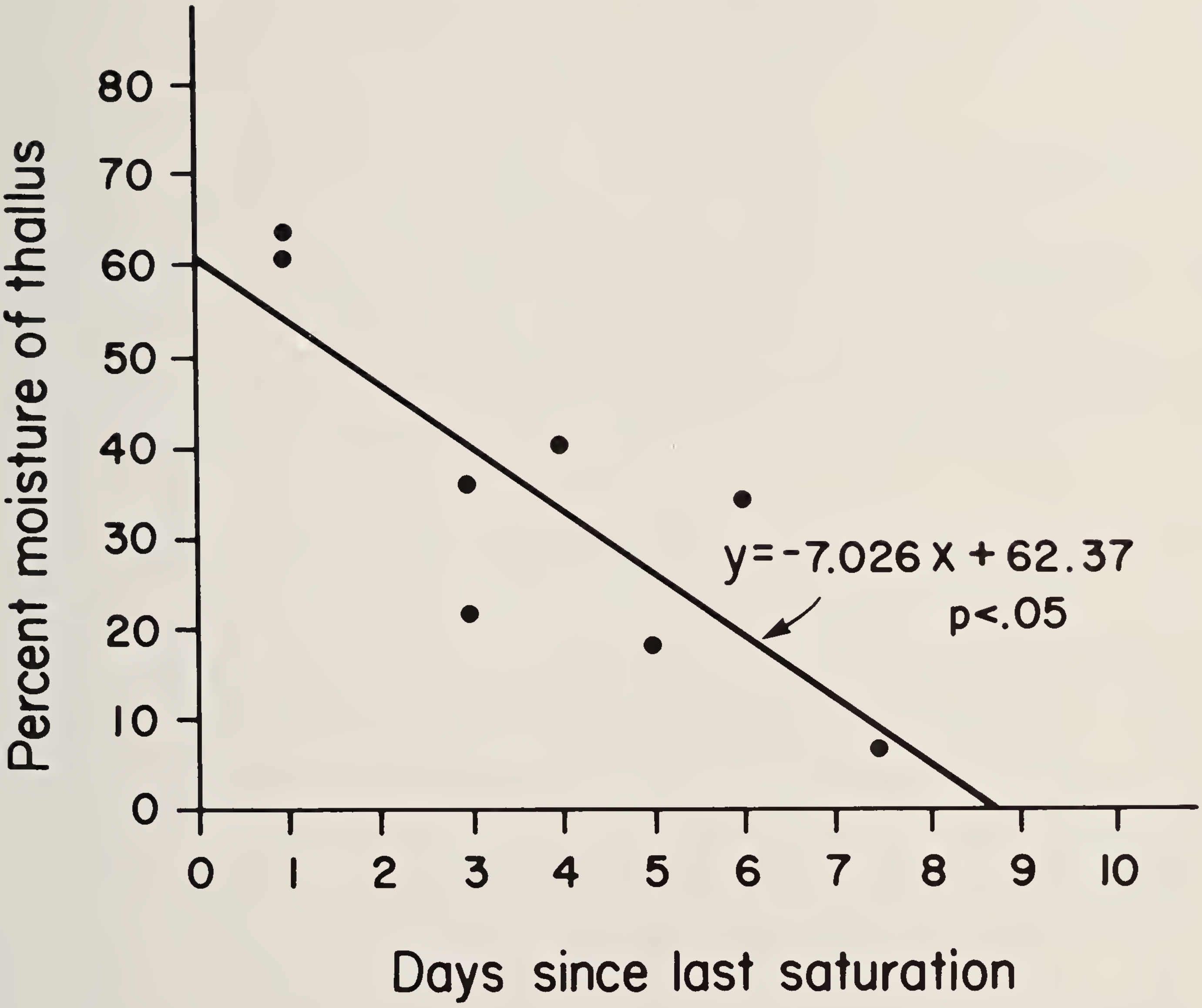


Fig. 2. Moisture content of lungwort thalli collected from *Acer rubrum* at various intervals after saturating rainfall, June, 1978.

Table II. Summary of *Acer rubrum* census

Quadrat (400 m^2)	No. *Acer rubrum* stems (over 5 cm DBH)	No. *Acer rubrum* stems with lungwort
1	21	9
2	3	2
3	17	9
4	36	4
5	16	0
6	52	10
7	10	2
8	12	3
9	36	7
10	25	6
Total	228	52.0

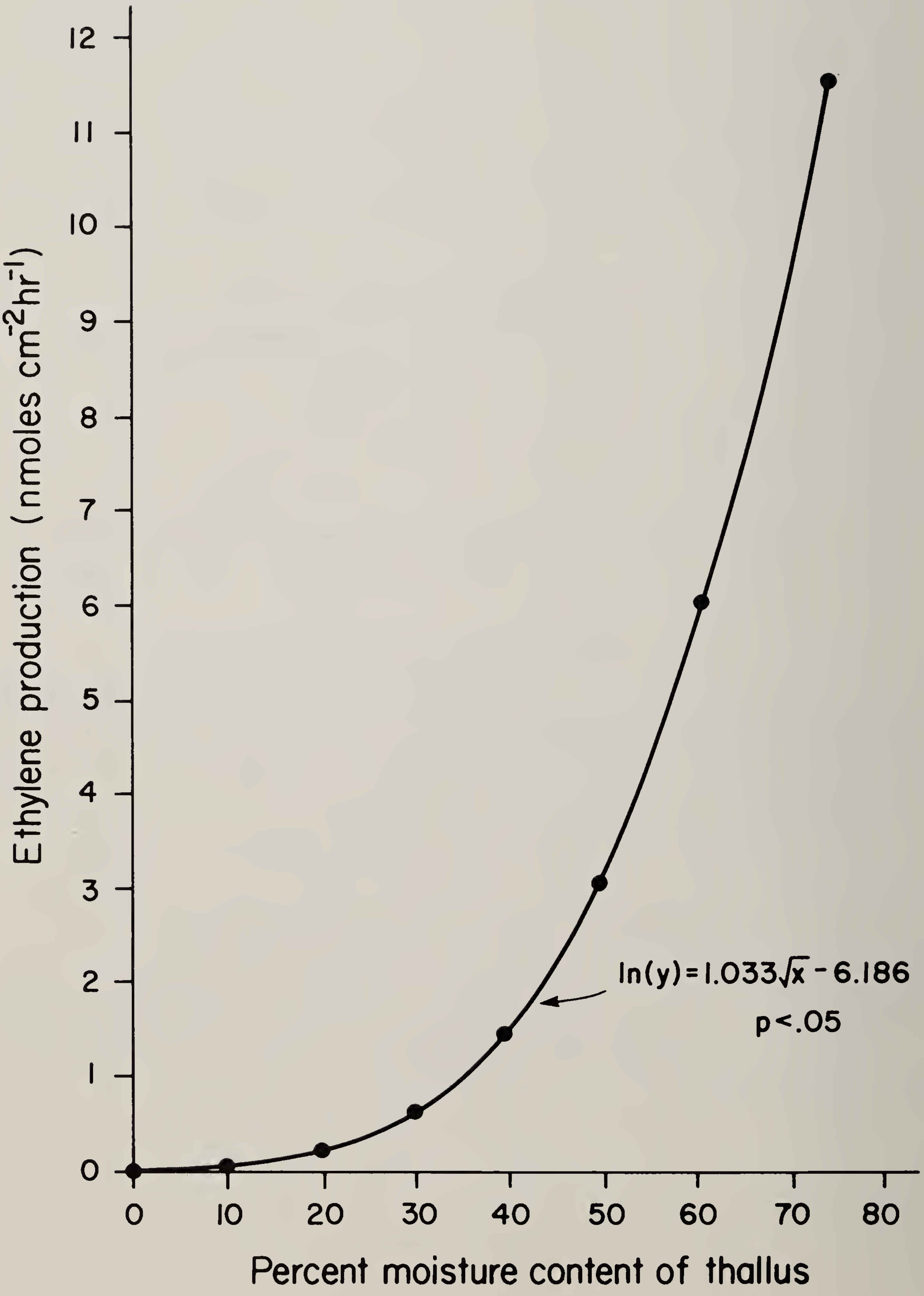


Fig. 3. The relationship between nitrogenase activity and thallus moisture content estimated from data of June, 1978.

The sum of the ethylene production values for each month was multiplied by this value to give the total amount of fixation for that period. It was assumed that fixation which occurred in darkness was equal to the amount lost during the nitrogenase lag phase experienced upon re-illumination.

The effect of seasonal temperature variations on nitrogenase activity was approximated in the calculation by multiplying the total N_2 fixation for each month by a temperature correction factor. This factor was determined from a Q10 value calculated from the differences in nitrogenase activity at 3° and 15°C (Fig 4) when moisture contents were equivalent, and utilized the mean daytime temperature for each month. The temperature corrected, total ethylene production figures for each month were converted to nitrogen fixation values and summed (Table III). The Q10 value was used without reference to a critical minimum temperature below which no activity occurs.

Results

Ecology of Lungwort

Thorough inspection of all 10 quadrats indicated that lungwort occurred only on *Acer rubrum* stems (Fig 5-8 and Table II). The density of *Acer rubrum* was found to vary considerably between quadrats. Values ranged from 3 to 52 stems pvr 400 m^2. Lungwort occurred on 22.8% of *Acer rubrum* in the study area. Coverage values for individual stems also varied considerably. The mean value for coverage of stems with lungwort is 0.207 m^2 per stem. Stems with a larger DBH had a higher mean frequency of lungwort occurrence (Fig 5), but the 20 to 25 cm DBH class had the greatest mean coverage value (Fig 6). Lungwort coverage per stem was greatest in cases where 2 or 3 stems were produced from a stump (Fig 7).

The vertical distribution of lungwort indicates that it occurs close to the forest floor. Sixty percent of lichen coverage was within 1 m of the ground and a 10-m height encompassed 96% of coverage (Fig 8).

Table III. Monthly estimates of nitrogen fixed by lungwort (1978)

Month	μg N fixed cm^{-2} lichen	gN fixed ha^{-1} forest
January	1.01	0.128
February	0*	0
March	1.40	0.178
April	3.58	0.455
May	4.08	0.519
June	5.46	0.693
July	3.97	0.505
August	0*	0
September	3.75	0.477
October	2.66	0.338
November	.76	0.096
December	1.12	0.142
Year Total	27.80	3.531

*The actual values could be as high as 1.01 for February and 3.75 for August.

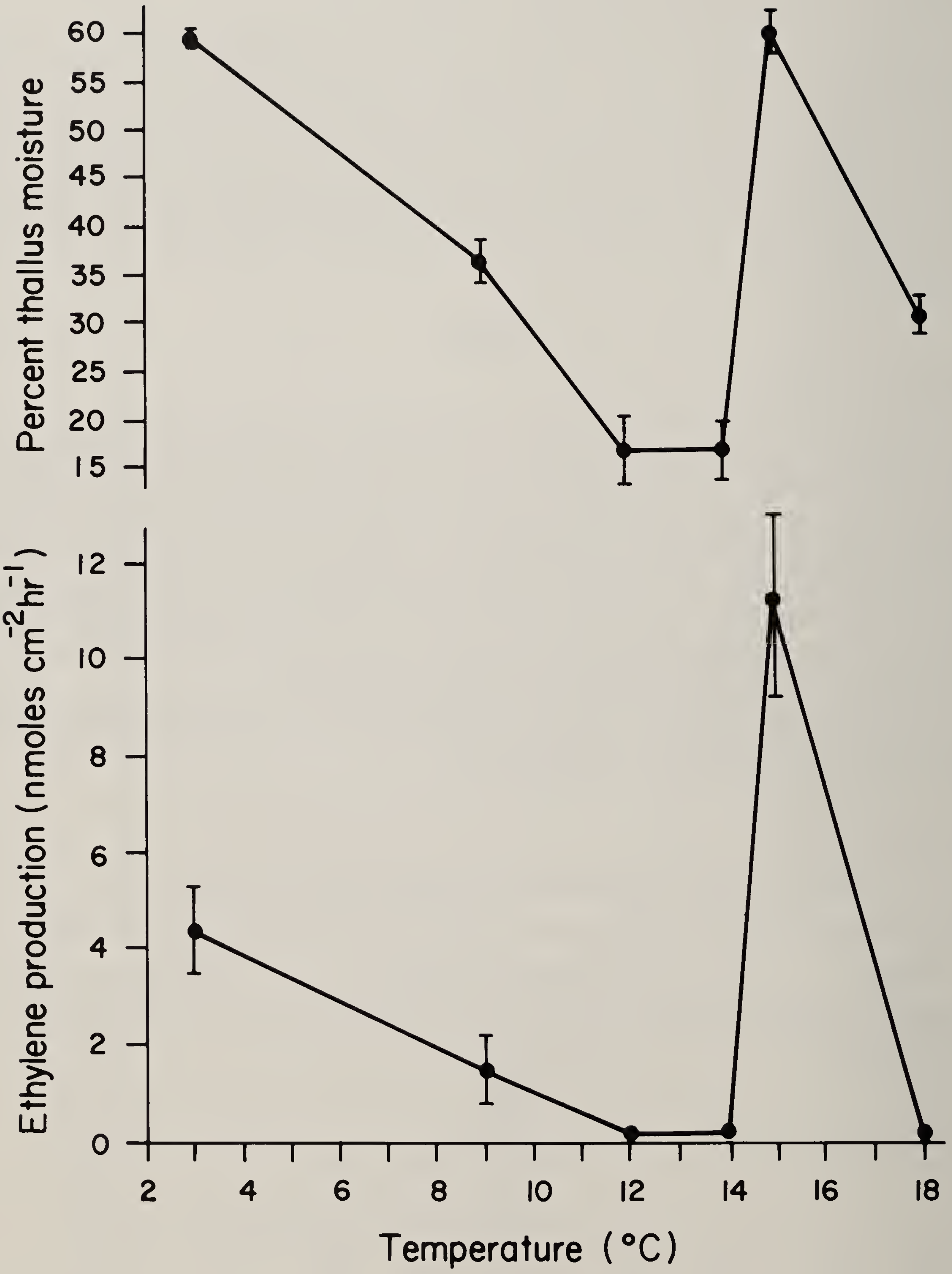


Fig. 4. Thallus moisture content (top) and nitrogenase activity (bottom) on days of different temperature. A Q_{10} factor for nitrogenase activity was calculatged from the nitrogenase activities at 3° and 15°C, when moisture contents were equivalent. Bars indicate standard deviations.

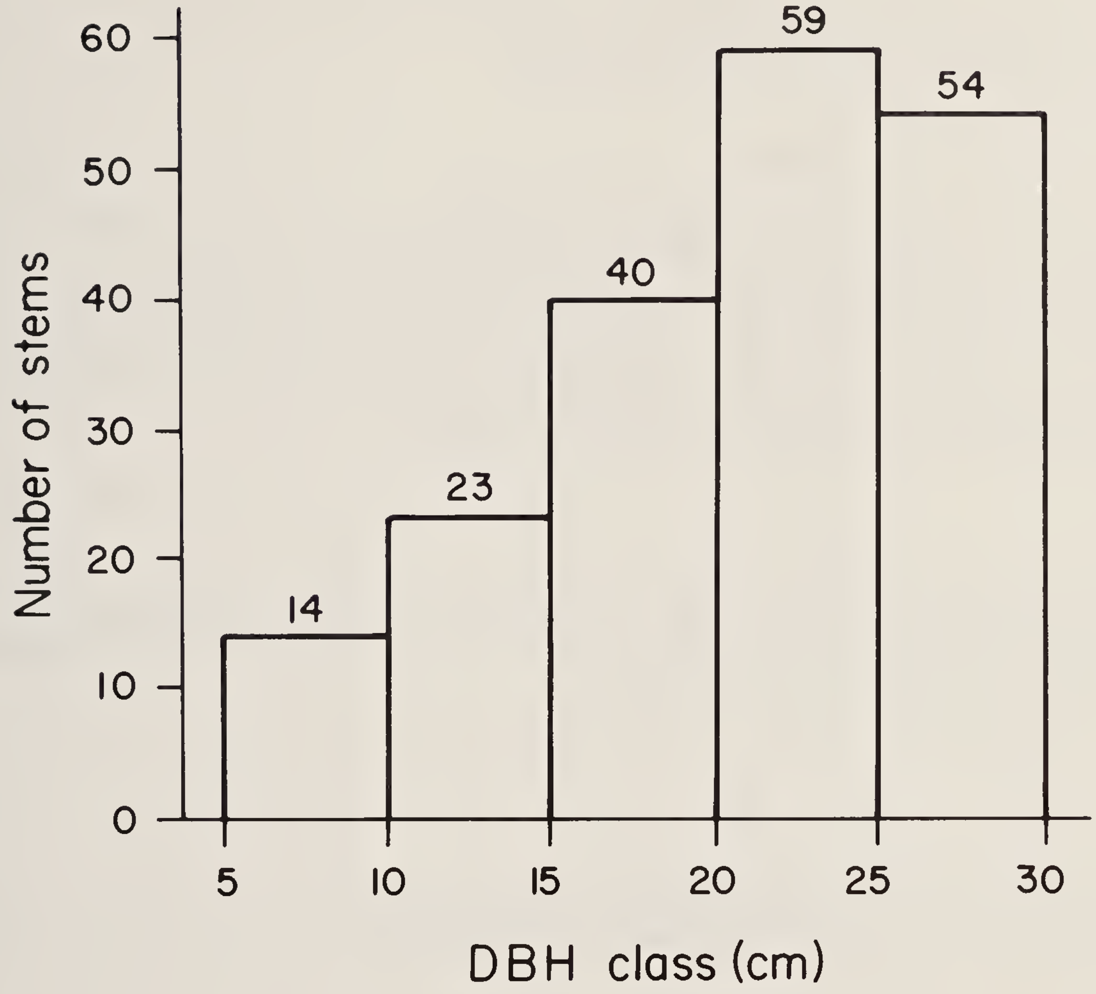


Fig. 5. Frequency of lungwort on *Acer rubrum* stems of different diameters.

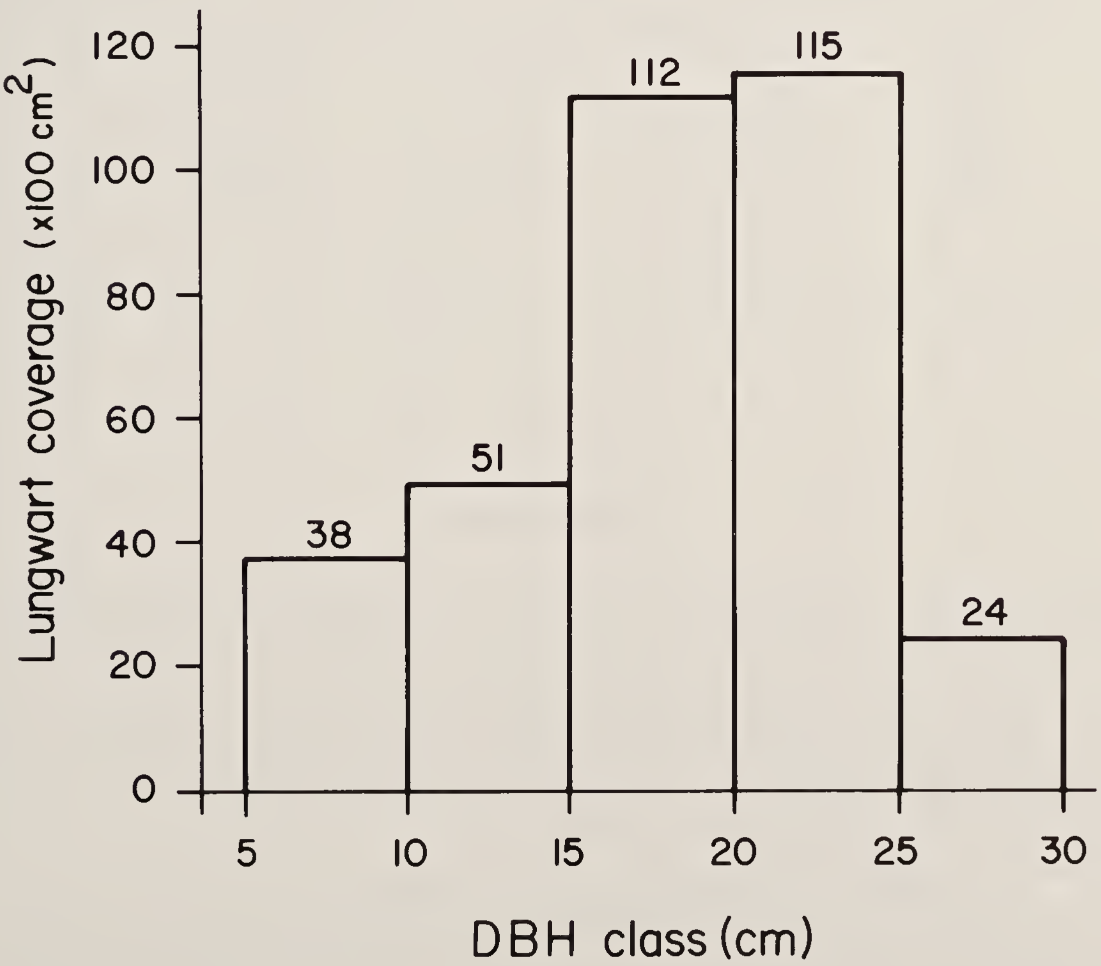


Fig. 6. Lungwort coverage on *Acer rubrum* stems of different diameters.

From the data collected in the study area, it is estimated that lungwort coverage in this area is 5.075 m^2 or 12.7 m^2 per hectare.

Nitrogenase Activity of Lungwort

The results of the acetylene reduction assays were extremely variable. Figure 4 indicates that the activity is closely correlated with the moisture content of the thallus. Figure 3 illustrates the calculated relationship between thallus moisture and nitrogenase activity for lungwort collected in June. The enzyme was found to be active in spring, autumn, and winter with the second highest activity reading occurring in February 1979 after a period of intense rainfall.

Stemflow

Results of the analysis for nitrogen content of stemflow and throughfall samples are presented in Table IV. These data support the contention that nitrogen is added to the rainfall as it flows down the trunk.

Table IV. Kjeldahl nitrogen in stemflow samples collected from *Acer rubrum* stems with lungwort cover, and throughfall samples collected under the *Acer rubrum* canopy

Collection Date	Quadrat	Throughfall mgN/50 ml	Stemflow no Lichen mgN/50 ml	Stemflow over Lichen mgN/50 ml	Apparent nitrogen accumulation mgN/50 ml
08/06/78	3(A)	107.7	103.9	138.8	+34,9
08/06/78	4(B)	43.3	57.2	76.2	+19.0
13/06/78	9(C)	27.5	75.5	178.2	+131.1
13/06/78	10(D)	22.0	75.5	73.3	-2.2*

*This negative value possibly an experimental error.

Discussion

Nitrogenase activity was observed to vary considerably between sample assays. However, a close correlation between moisture content and activity was observed. Results are in agreement with work done on other lichen species by Hitch (1971), Hitch and Stewart (1973), and Kershaw (1974) in that thallus-moisture content is the most important environmental factor affecting activity. Recovery of activity after periods of desiccation were also observed.

Temperature was also found to influence nitrogenase activity. Comparison of activity from June and February with comparable thallus-moisture contents showed a 68% drop in nitrogenase activity with a 12°C drop in temperature (Fig 4). Winter results for lungwort activity contrast with those of Kelly and Becker (1975) who detected no nitrogenase activity in temperatures under 10°C.

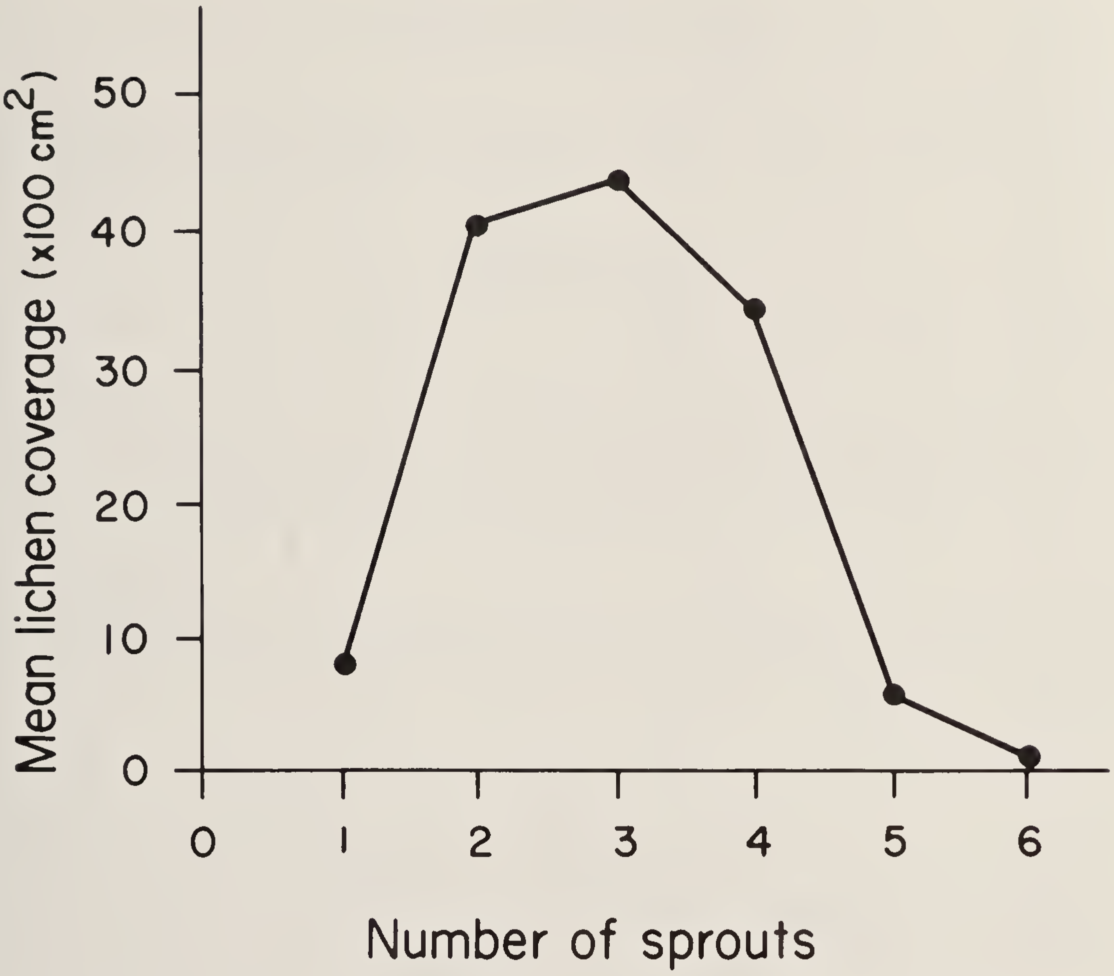


Fig. 7. Lungwort coverage in relation to number of *Acer rubrum* stump sprouts.

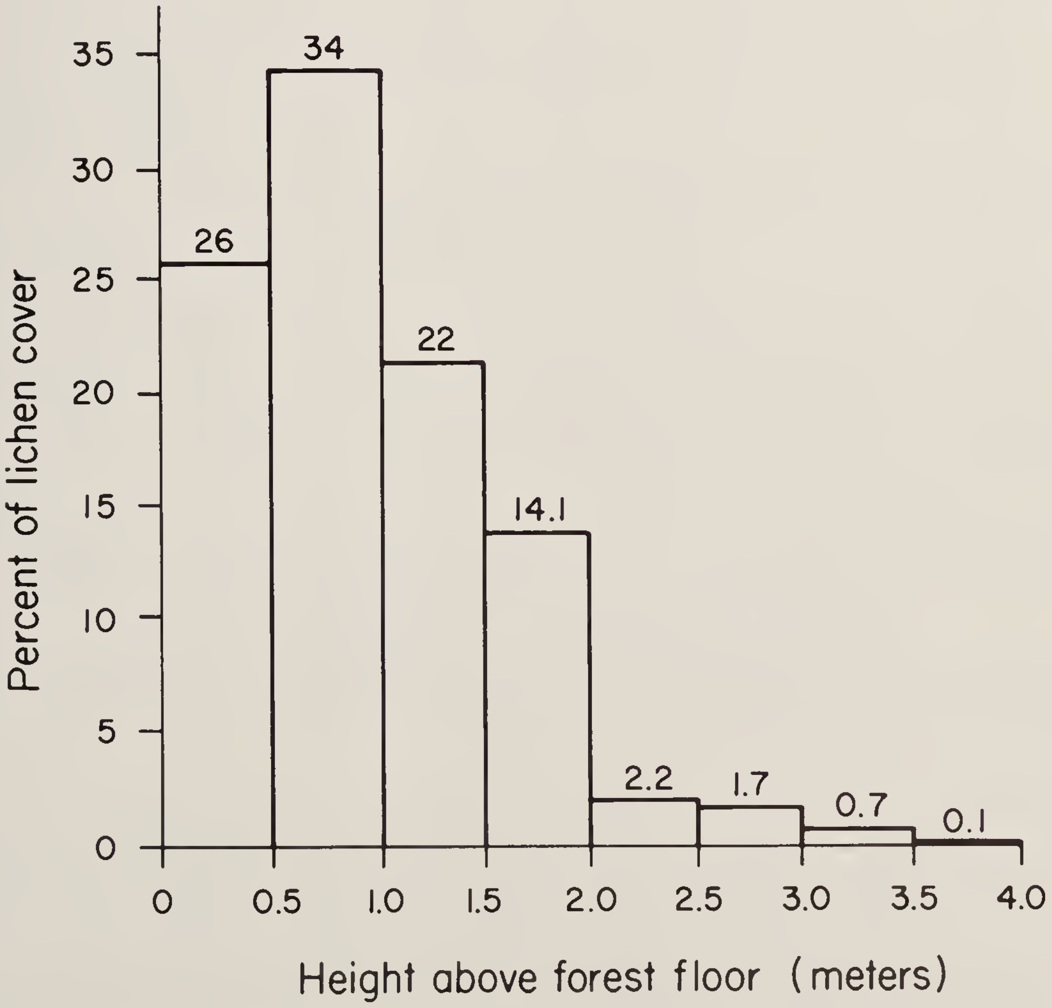


Fig. 8. Percentage of total lichen cover in successive 0.5-m intervals above the forest floor.

Monthly climatic variations cause N_2 fixation results to be sporadic. Estimated N_2 fixation for February is indicated as zero in Table III because the month was cold with most of the precipitation occurring as snow. However, the readings which were obtained in that month suggest that at least on some occasions high rates of N_2 fixation are possible. Therefore, the yearly total is calculated assuming the lowest possible value figure although likely it is as high as that for January. Estimated N_2 fixation for August was zero as rainfall was insufficient to saturate the thallus. The period of greatest fixation predicted by the calculations is in the late spring and early summer.

Annual predictions of nitrogenase activity for lungwort indicate that about 3.53 gN ha^{-1} could be fixed annually. Soil analysis for this region indicate a nitrate value of 2 kg ha^{-1} (N.S. Dept. Agric.). Atmospheric washout adds from 2 to 10 kg of nitrogen per hectare (Russel 1961). Thus 3.53 gN ha^{-1} represents 0.176% of the nitrate-nitrogen in the soil, and the minimum amount of nitrogen added by precipitation is similar. 3.53 gN ha^{-1} yr^{-1}, though low, is 2.9 times greater than the fixation reported by Becker et al. (1977) for all nitrogen-fixing lichens in a North Carolina oak-hickory forest.

Since the influence of stemflow on soil properties is limited to 30 cm from the tree stem (Voigt 1960), we investigated whether the N_2 fixation by the amount of lungwort present on 1 tree, is of significance to the nitrogen budget of that tree. For these calculations, an average and the maximum lungwort coverage values for the stems in the study area were used. The average coverage of lichens could only fix N_2, equivalent to about 0.6% of the annual increase in nitrogen content of the stems. The maximum amount of lungwort on a stem could possibly fix N_2 equivalent to 4.9% of the nitrogen content of the foliage. Thus fixation by lungwort appears to be of limited significance to the nitrogen budget of the *Acer rubrum* tree. Results of the stemflow and throughfall analysis for nitrogen are in agreement with Kittredge (1948), Will (1955), and Voigt (1960) in that rainwater samples which had flowed over the stem became enriched in nitrogen. The nitrogen concentration of stemflow was found to vary considerably between *Acer rubrum* stems (Blacklock 1979).

The collection at site D was different from the others in that stemflow which did not pass over lungwort was collected first (Table IV). This was the only site where there was no net increase in nitrogen when stemflow was allowed to pass over lungwort. Gersper and Holowachuk (1971) found the initial flush of stemflow has a higher concentration of nutrients than subsequent flow resulting from washing of particulate matter from the foliage and bark. Hence it is possible that the estimated nitrogen contribution by lungwort to stemflow on the tested stems is biased with estimates of accumulation for quadrats A to C being too high.

If it is assumed that the mean difference in nitrogen in stemflow samples results from leaching from lungwort and the leaching rate is constant, then 0.114 g yr^{-1} of nitrogen may be contributed to stemflow by the average amount of lungwort on an *Acer rubrum* stem. The total estimated input of nitrogen by stemflow is .218 gN per tree which is about 2.2% of the tree's annual nitrogen addition to biomass. Thus stemflow does not appear to be a significant source of nitrogen for *Acer rubrum* in this area.

According to Denison (1973), the major flux of nitrogen from lichens to the ecosystem is via litter fall. Using a 2.7% nitrogen content (dry wt) for lungwort and a conversion of 1 g lungwort being equivalent to 40 cm^2, the total amount of nitrogen incorporated in lungwort biomass is 86 g ha^{-1}. Using even a generous decomposition rate of 10% (Barkman 1958), it is evident that lungwort litter fall would not be an important source of nitrogen in the forest, as it would amount to only 0.75% of the nitrogen available from *Acer rubrum* leaf litter.

Acknowledgements

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ANGIOSPERM PRODUCTIVITY IN TWO SALTMARSHES OF MINAS BASIN*

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Above-ground angiosperm productivity in 2 saltmarshes of Minas Basin (Bay of Fundy) was estimated at about 500 g dry wt m^{-2} yr^{-1}, a low value compared with marshes on the Atlantic coast of Nova Scotia. Below-ground production may provide an additional 900 g dry wt m^{-2} yr^{-1}. The percentage carbon in the plants was low, about 34% of the dry weight. The addition of NH_4NO_3 to marsh soils increased the above-ground productivity by about 90% despite the high levels of NO^-_3 and NO^-_2 previously reported for these marshes. Three species of angiosperms, *Juncus gerardii, Spartina patens,* and *Spartina alterniflora,* were dominant. All of the standing crop of *S. alterniflora* was transported from the marshes to the surrounding estuarine waters early in the autumn. Standing crop of the other 2 species, as well as below-ground production of all 3 species, remained on the marshes. Shading by the angiosperm canopy had a significant effect on the soil temperature.

Introduction

Saltmarshes in temperate latitudes along the Atlantic coast of North America are highly productive (Odum 1971; Seneca 1974), with much of this production being transported into surrounding waters (Teal 1962) where it forms an important source of nutrients (Teal 1962; Reed & Moisan 1971; Mann 1975). It has been demonstrated (Turner 1976) that energy incident on a saltmarsh area and angiosperm productivity are generally correlated, with productivity decreasing as latitude increases. On the Atlantic coast of Nova Scotia, relatively high levels of productivity were recorded in saltmarshes dominated by the grass *Spartina alterniflora* (Martin 1974; Hatcher & Mann 1975; Livingstone 1978; Patriquin & McClung 1978).

The Bay of Fundy, between Nova Scotia and New Brunswick, is characterized by very large-amplitude tides, rapid tidal currents and high levels of suspended matter (Bousfield & Leim 1960; Dalrymple et al. 1975; Pelletier & McMullen 1972). At the head of the bay, on the soft sediments of Chignecto Bay and Minas Basin, extensive saltmarshes occur. Apart from the study of Morantz (1976) in Cumberland Basin, the productivity of these marshes, which exist under unique physical conditions, has not been examined. The present paper reports on productivity of 2 saltmarsh systems in Minas Basin.

Materials and Methods

Study Areas and Transects

Transects were established on 2 saltmarshes in Kings County, Nova Scotia. One marsh, near Grand Pré, has existed only 15 years, because of recent dyking, and consists almost entirely of a single species, *Spartina alterniflora;* the other marsh, near Kingsport, is an older community with several distinct vegetational zones. Along each transect, 4 floristic zones were recognized, as determined by species dominance at Kingsport, and by growth forms of the single dominant at Grand Pré; one sampling station was established near the middle of each zone. Fertilization experiments were conducted in 1979. All other data were collected biweekly during the summer of 1978.

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Angiosperm Productivity

Above-ground angiosperm production was measured by quantifying standing crop. Aerial portions of plants were clipped from 0.0625-m^2 quadrats (0.25 m x 0.25 m) randomly positioned near the sampling stations. Three quadrats were harvested at each sampling station on each sampling day. Samples were washed, sorted into living and dead material, dried for 48 h at 105°C, and weighed. Peak above-ground biomass was used to estimate annual production, subject to correction for minor losses of lower leaves in the case of *Spartina alterniflora* (Morantz 1976). Average height of plants was approximated for correlation with biomass.

Fertilization Experiments

Early in June, 2 plots 9 m^2 (3 m x 3 m), experimental and control, were established in each floristic zone. The experimental plot of each pair was fertilized with 500 g NH_4NO_3 (165 kg N ha^{-1}); premeasured amounts of the fertilizer were poured into 100 evenly spaced holes, 1 dm deep, made with a steel rod of 1 cm diameter.

Light Extinction

The relative intensity of light reaching the soil surface was determined in all productivity quadrats prior to harvesting. The light intensity above the angiosperm canopy was also measured. These values were applied to the expression

$$\text{Fractional light extinction} = (h\nu_a - h\nu_b)/h\nu_a$$

where $h\nu_a$ = light intensity above the angiosperm canopy and $h\nu_b$ = light intensity at the mud surface beneath the canopy. Light intensity was measured with a Li-Cor LI-185 meter equipped with a quantum sensor.

Temperature

Air, soil surface, and subsoil (-10 cm) temperatures were taken at each sampling station on each sampling day. Temperature determinations were made with a YSI Model 44 electric telethermometer.

Carbon Determination

Carbon was determined, in 18 randomly selected angiosperm samples, by C, H, N analysis, and is expressed as percent of the dry weight.

Results

Flora

The plants observed in each transect are indicated in Table I and Figures 1 and 2. The total dominance of *S. alterniflora* at Grand Pré results from the high frequency of tidal inundation, the marsh being completely flooded on all but the lowest high tides. This, in turn, is because of the relative youth of the Grand Pré marsh, and possibly this marsh is still accreting.

Angiosperm Productivity

Above-ground productivity at Kingsport by *J. gerardii* (zone 1) and *S. patens* (zones 2 and 3) was similar (Table II). Production by *S. alterniflora* (zone 4 of Kingsport and all zones of Grand Pré; Table II) was about 20% higher than that of *J. gerardii* and *S. patens*. Substantial variation in the productivity of the growth forms of *S. alterniflora* was observed. Stands at the edges of channels (zones 1 and 4 at Grand Pré

Table I. Description of the zones established in the Grand Pré and Kingsport marshes

Grand Pré	Location along Transect (m)	Angiosperm Vegetation
Zone 1	5.5-23	Late-flowering and tall *Spartina alterniflora* Loisel. (112 cm).
Zone 2	23-44 and 0-5.5	Early-flowering (shortly before Zone 1) *Spartina alterniflora* (46 cm); scattered *Suaeda maritima* (L.) Dumort., *Salicornia europaea* L., *Limonium nashii* Small., and *Triglochin elata* Nutt.
Zone 3	44-75	Shortened (61 cm), sparse *Spartina alterniflora,* flowering between Zones 1 and 2.
Zone 4	75-133.5	Tall (84 cm) and dense *Spartina alterniflora;* flowering as in Zone 1.
Kingsport		
Zone 1	0-28	*Juncus gerardii* Loisel. (51 cm) with *Spartina pectinata* Link and *Agropyron repens* (L.) Beauv. near upper limits.
Zone 2	28-45	*Spartina patens* (Ait.) Muhl. (43 cm) dominant; few other angiosperms.
Zone 3	43-83.5	*Spartina patens* (39 cm) with uniform mixture of *Plantago maritima* L. and *Puccinellia americana* Soer.; *Spartina alterniflora* and *Triglochin elata* occasional throughout; *Salicornia europaea, Suaeda maritima* and *Atriplex patula* L. occasional in lower portion only.
Zone 4	83.5-95.5	*Spartina alterniflora* dominant (69 cm) but not dense.

Table II. Angiosperm production of the Kingsport and Grand Pré saltmarshes in g dry wt m^{-2} yr^{-1}

	Kingsport			Grand Pré		
Zone	Date[1]	Above-Ground	Below-Ground	Date[1]	Above-Ground	Below-Ground
1	May 28	473	827	July 12	816	1429
2	Aug 8	479	838	July 27	408	714
3	Aug 8	491	859	July 27	354	619
4	July 27	609	1065	Aug 8	684	1197
Entire Transect		499	873		570	998

[1] Date when maximum above-ground standing crop was measured

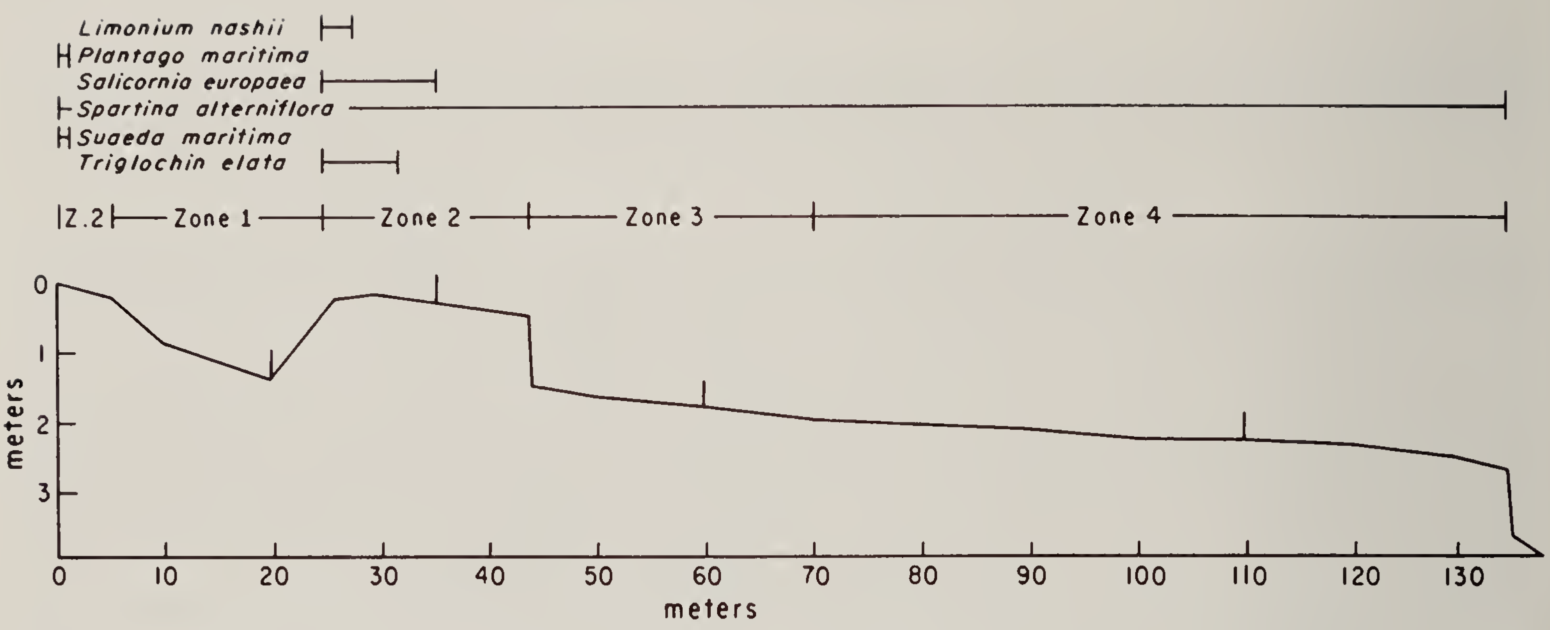

Fig 1. Profile of the Grand Pré transect. The 4 floristic zones and the distribution of the various angiosperm species are indicated by the horizontal bars above the profile. The 4 vertical bars on the marsh surface indicate the location of the sampling stations.

and zone 4 at Kingsport) were taller and exhibited much higher productivity than adjacent shorter growth; at Grand Pré production in zone 1 was more than twice that of zone 2 or 3 (Table II). In fact, there was close correlation between height and biomass throughout the 2 marshes (Table III). The lowermost zones, bordering the estuary (zone 4), showed similar productivity at both marsh sites (Table II). Overall production was slightly greater at Grand Pré, reflecting the higher productivity of *S. alterniflora* (Table II).

Lower leaves of *S. alterniflora* began to die before peak biomass had been reached (Fig 3c), although dead leaves with intact leaf bases persisted on the culms to soil surface level throughout the sampling period. Most of the above-ground production of *S. alterniflora* was, however, swept off the marshes by early December, before the occurrence of any ice-scouring. For these reasons the annual above-ground production in zones dominated by *S. alterniflora* was estimated from the highest total mass sum of live and dead material during the season. In contrast, dead material from previous growing seasons persisted, in large quantities, in areas dominated by *S. patens* and *J. gerardii* (Fig 3a, b), and current growth did not begin to die until maximum biomass was attained. Thus, annual production of *S. patens* and *J. gerardii*

Table III. Correlation between plant biomass and height on the Grand Pré and Kingsport saltmarshes

Zone	Slope	Y intercept	R	R^2
Grand Pré				
1	2.05	4.99	0.91	0.82
2	1.92	6.65	0.87	0.75
3	2.79	3.86	0.99	0.97
4	2.06	1.00	0.99	0.97
Kingsport				
1	1.29	7.91	0.88	0.80
2	0.89	15.63	0.98	0.96
3	0.91	13.96	0.96	0.91
4	1.80	15.04	0.89	0.80

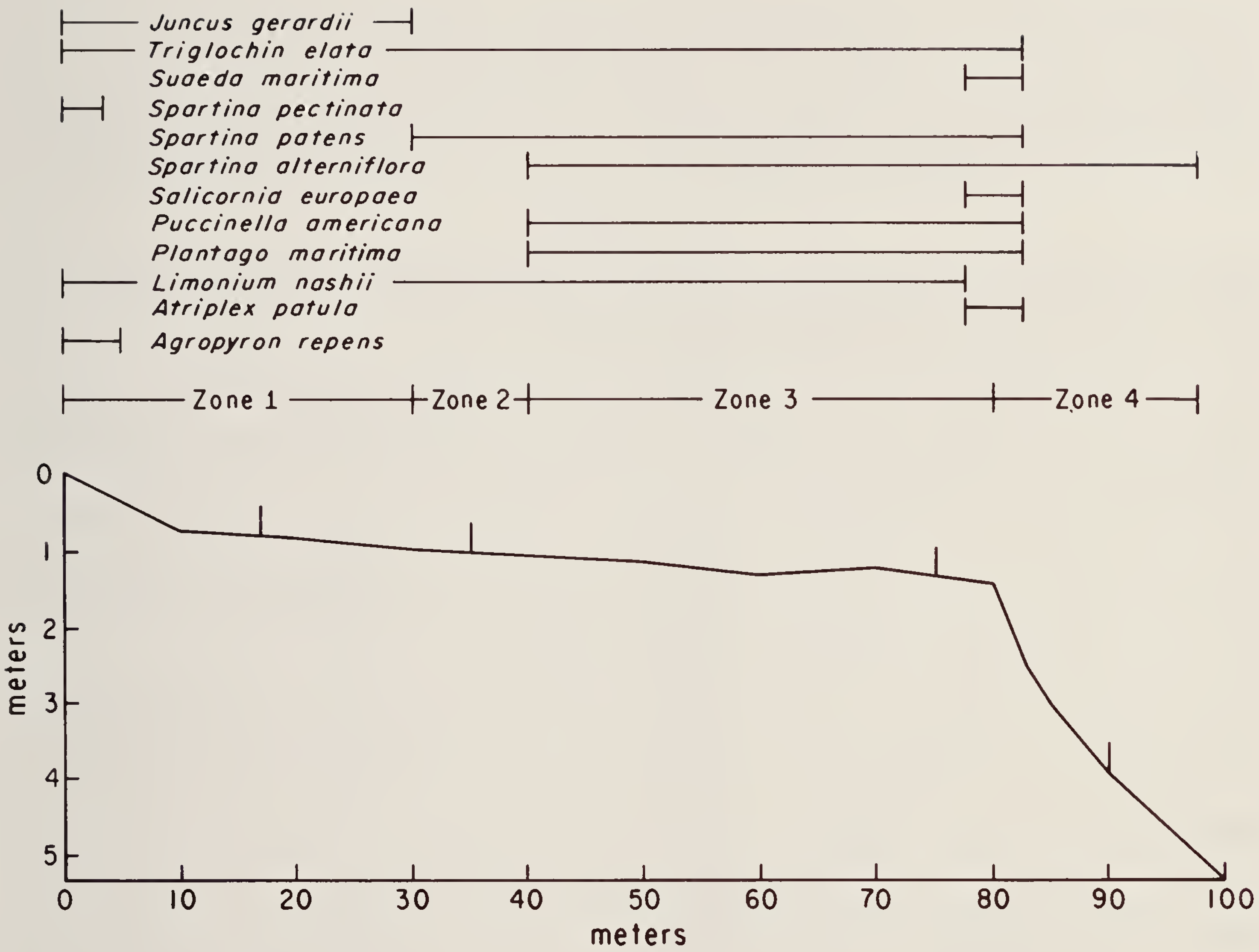

Fig 2. Profile of the Kingsport transect. The 4 floristic zones, the distribution of the various angiosperm species, and the sampling stations are indicated as in Fig 1.

was estimated from the weight of living material only. Below-ground production (Table II) was estimated by multiplying above-ground values by 1.75 (Patriquin & McClung 1978).

Addition of NH_4NO_3 to saltmarsh soils increased the above-ground production of angiosperms by an average of 88%. The increase was large and statistically significant in all zones except zone 2 of the Kingsport marsh (Table IV). Fertilization did, however, have a positive effect on *S. alterniflora* which is scattered on the order of several shoots per m^2 in this *S. patens* community. These plants normally are small and fail to flower, but inside the fertilized plot they were robust and completed the normal reproductive cycle.

The average percentage of carbon in plants on the 2 marshes (1978, unfertilized) was 34.4 3.6% ($n = 18$). There was little variation among species or throughout the season. This percentage of carbon is considerably lower than the 40.77% for *S. alterniflora* reported by Burkholder and Bornside (1957).

Light

Generally, a good correlation existed between the height of angiosperms and the fractional light extinction by the plant canopy (Table V), except in zones dominated by *S. patens* (Kingsport zones 2 & 3). These zones retained a dense canopy of dead plants from the previous growing season, resulting in high light extinction throughout the summer. As angiosperm height and biomass correlated very well (Table III), light extinction therefore may be viewed as a function of either factor.

A strong negative correlation existed between fractional light extinction and soil temperature (Table VI). Although there was no significant difference in air temperatures over the 2 marshes, the average soil surface and subsoil temperatures were both slightly lower at Kingsport (Table VII). This is probably due to the greater light extinction by canopy of *J. gerardii* and *S. patens* (Kingsport zones 1-3, Table VI).

Table IV. Effects of application of NH_4NO_3 on angiosperm above-ground production in the Grand Pré and Kingsport saltmarshes

Zone	N[1]	Mean[2] g Dry Wt m^{-2}	2 Standard Error Units	% Increase
Grand Pré				
1	+	761.6	57.8	45.1
	-	524.8	62.2	
2	+	620.8	53.2	41.6
	-	438.4	99.6	
3	+	372.8	62.2	137.7
	-	156.8	38.4	
4	+	710.4	106.4	48.5
	-	478.4	34.0	
Kingsport				
1	+	846.4	184.4	128.0
	-	371.2	43.0	
2	+	519.2	207.0	9.8
	-	472.8	141.4	
3	+	809.1	138.0	173.8
	-	295.5	41.8	
4	+	675.2	167.4	117.5
	-	310.4	49.8	

[1] + values are from fertilized (NH_4NO_3) plots; - values are from control plots
[2] n = 8

Table V. Correlation between plant height and light extinction on the Grand Pré and Kingsport saltmarshes

Zone	Slope	Y intercept	R	R^2
Grand Pré				
1	0.025	0.63	0.87	0.76
2	0.006	0.05	0.71	0.50
3	0.006	0.43	0.74	0.58
4	0.005	0.53	0.86	0.73
Kingsport				
1	0.009	0.47	0.85	0.73
2	0.005	0.68	0.50	0.25
3	0.003	0.80	0.50	0.25
4	0.011	0.10	0.91	0.84

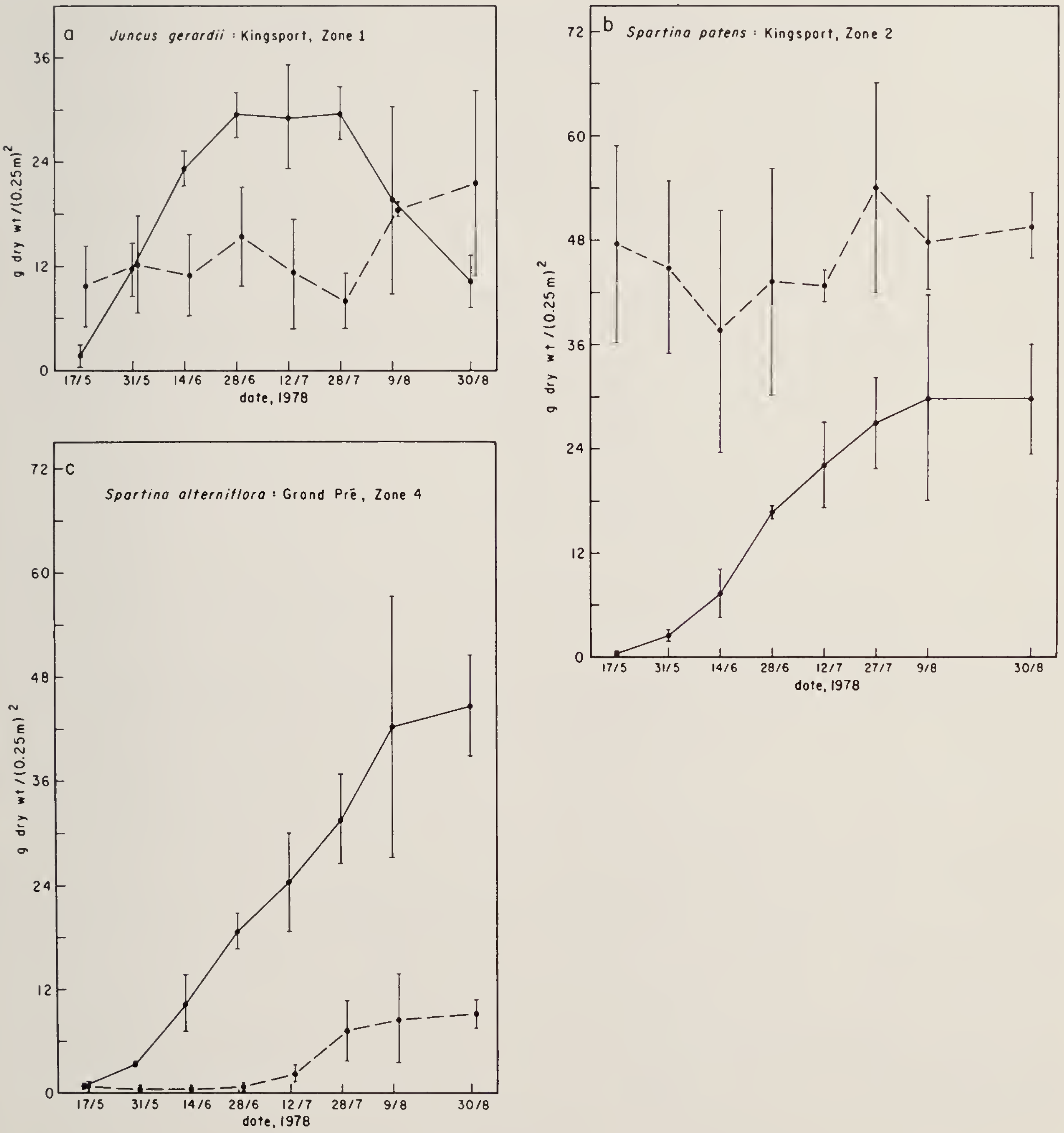

Fig 3. Seasonal distribution of live (—) and dead (--) angiosperm material in marsh communities dominated by (a) *Juncus gerardii,* (b) *Spartina patens,* and (c) *Spartina alterniflora.* Each point is the average of 3 measurements. Vertical bars indicate ± 2S $\bar{x}$.

Table VI. Correlations between light extinction and subsurface (-10 cm) soil temperature, based on the averages of each zone over the entire summer[1]

Grand Pré

Zone	Temp. (°C)	Light Extinguished		Slope	Y intercept	
1	16.0 ± 2.6	0.71	0.12	6.59	20.8	-0.84
2	17.1 ± 3.0	0.56	0.12			
3	16.9 ± 3.2	0.66	0.08			
4	16.4 ± 3.4	0.64	0.11			

Kingsport

Zone	Temp. (°C)	Light Extinguished		Slope	Y intercept	
1	14.3 ± 3.1	0.78	0.08	2.15	15.6	0.81
2	13.7 ± 2.9	0.80	0.09			
3	13.6 ± 2.9	0.90	0.05			
4	14.4 ± 3.1	0.53	0.14			

[1] All values given with a ± 2S $\bar{x}$ estimate of sample variation (n = 21)

Table VII. Comparisons of various parameters measured dn the Grand Pré, Kingsport, and other saltmarshes

Parameter	Grand Pré	Kingsport	Other
% light extinction[1]	0.64 ± 0.05	0.79 ± 0.05	
soil surface temperature[1] (°C)	21.9 ± 1.7	18.4 ± 1.3	
subsoil (-10 cm) temperature[1] (°C)	16.6 ± 1.4	13.9 ± 1.1	
above-ground angiosperm biomass[2] (g dry wt m^{-2} yr^{-1})	529.8	492.8	750 (Martin 1974) 710 (Hatcher & Mann 1975 483 (Morantz 1976)

[1] mean value for the entire summer sampling period (1978)
[2] calculated from seasonal maxima

Discussion

Compared with marshes on the Atlantic coast of Nova Scotia, productivity in Minas Basin marshes was low (Table VII). The reasons for these low values are unclear, but the dramatically different tidal regime — irregular and brief inundation of marshes, especially high marsh — is undoubtedly nutrient-limiting and has been suggested as contributing to lower overall productivity of marshes in the Bay of Fundy (Morantz 1976). Enhancement of above-ground production by addition of nitrogen suggests that this element may be limiting, although previous data (Smith et al. 1979) showed that NO_2^- and NO_3^- nitrogen were present in high concentrations. Indeed, these levels are sufficient to inhibit biological nitrogen fixation. If nitrogen is limiting, the situation is paradoxical: starvation in the midst of plenty. Similar phenomena have been reported for saltmarshes on the Atlantic coast of the United States (Morris 1978; Mendelssohn 1979). Smith et al. (1979) found low levels of NH nitrogen in Minas Basin saltmarshes, and high ammonium concentrations are reported for Massachusetts saltmarshes (Valiela et al. 1975). On the Atlantic coast of Nova Scotia, high concentrations of NH_4^+ nitrogen were observed in a high marsh situation (Patriquin & Keddy 1978), but low concentrations of NH_4^+ and NO_3^- nitrogen in the low marsh (Livingstone 1978). High nitrite levels (Smith et al. 1979) had not been previously reported in saltmarsh soil water, and these levels observed in the study area may indicate some type of blockage in the oxidization or reduction of nitrite. Such a blockage could play a role in the apparent nitrogen limitation. However, the precise cause of nitrogen limitation is uncertain and is the current subject of investigation by various workers (e.g. Mendelssohn 1979). Another factor which may have limited productivity is extreme anaerobiosis of the fine clay substrate, producing an oxygen limitation around plant roots.

Spartina alterniflora in Bay of Fundy marshes differs from that in marshes on the Atlantic coast of Nova Scotia with respect to export of biomass during the growing season. Hatcher and Mann (1975) reported losses of older leaves in Atlantic coast plants to the extent of 23.3 to 35.1% of annual above-ground production. Morantz (1976), however, found that about 12% of plants sampled in mid-summer displayed abscission of lower leaves, and calculated a net loss during the growing season of only 6.8%. Although *S. alterniflora* in the present study had intact lower leaf bases to soil surface level, the decreasing proportion of dead material during August (Fig 3c) suggest that minor attrition of older material, whether as entire leaves or their distal portions, was occurring, and production values for this species are probably slightly underestimated.

The year-round presence of large amounts of dead angiosperm material in zones 1, 2, and 3 of the Kingsport marsh (*S. patens* and *J. gerardii)* indicates that much of the production of these zones was not being exported to the estuarine waters. In contrast, nearly all annual above-ground production of *S. alterniflora* was exported from the marsh during October and November. Presumably all below-ground production remained on the saltmarshes and was slowly mineralized or buried. At Grand Pré, roots of *S. alterniflora* occurred at a depth of at least 1 m, and at the end of the transect was the exposed edge of an old saltmarsh root layer about 2 m below the current layer. This turf is probably the remains of the marsh which existed here prior to construction of the present dyke, and is indicative of the relative youth of the present marsh. Burial may also be related to the increasing tidal amplitude in the Bay of Fundy (Amos 1977).

The shading effect of the angiosperm canopy could exert a significant effect on algal, microbial, and invertebrate populations living on the mud surface. Lower subsoil temperatures under the dense *S. patens* and *J. gerardii* canopies of both living and dead material may have contributed to the lower production by these 2 species.

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PREFACE

The papers published in this issue of the **Proceedings** are based on lectures given by the authors in the 1979 - 1980 lecture series of the Institute. They are published because they review the present status of research and development in 4 of the basic industries of the Maritime Provinces. They should serve as a source of information to all concerned with economic growth and development in this region of Canada. The authors have spent most of their working lives intimately associated with the industries they describe, and their knowledge and experience is thus of great pedagogic value. The Institute is indebted to these scientists for the work they have done in preparing these papers and also wishes to record its appreciation to the organizations to which they are affiliated who have provided much support.

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THE NATURAL HISTORY OF FISHERIES MANAGEMENT

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The history of attempts at management of fisheries is presented. Current knowledge of the biology of fish populations is critically reviewed as such data have been the basis of schemes of management in the past. It is concluded that social, political, and economic factors are at least as important in fisheries management as the scientific knowledge of the resource.

Introduction

The 1970's have seen a global upsurge of interest in the subject of fisheries management to a degree exceeding anything previous. The fisheries of Atlantic Canada have played a leading role in the sequence of events that have generated this interest and, perhaps for the first time, there is now an awareness and a growing expectation here of the extent to which fisheries offer economic opportunities for the area as a whole. As a result, the management question is being studied by more and more individuals and groups representing a wide range of interests and disciplines. Inevitably, a "science" of fisheries management is being erected and attempts are being made to reduce the general question of fisheries management to elements that are amenable to formal analysis.

It is my belief that fisheries management represents such a complex mixture of certainty and uncertainty, dreams and realities, theory and actuality, that it is premature and even misleading to apply the term science to its practice. We should be content with the less prestigious but far more appropriate terms "natural history", with its connotations of judgement rather than deduction, assessment rather than analysis, and fore-sight rather than prediction. Why we should be relatively modest in our expectations, or rather realistic in our aims, can best be demonstrated by referring to 4 kinds of questions that can be asked of a fishery.

These can be arranged in a hierarchial series beginning with the simplest:

1) How many (or how much) fish? the biological resource question.
2) How many dollars? the economic question.
3) How many jobs? the social question.
4) How many votes? the political question.

At each of these levels, we can ask a further question: How are they allocated? This adds another degree of complexity, but even without this added degree, it must be conceded that one soon reaches the stage where formal scientific analysis must fail as a guide to decision and action. This is another way of saying that the theory becomes more and more divorced from reality.

Management Theory

Indeed, formal theory becomes less and less structured as you pass from one level to the next. Biological resource theory is by now very rich and detailed and has become tailored to deal with a wide range of situations.

There are two kinds of model in general use, the "biomass" or "logistic" type and the "analytical" or "dynamic pool" model, of which the second is the more detailed and sophisticated. The main stumbling block to a precise analytical assessment of stock resilience under fishing pressure is the "stock-recruitment" question. Every fishery reduces population size but there is no universal agreement on the effect of this on reproductive success and the ability of the reduced stock to replenish itself by "recruitment".

At the second level, the economic information required is both more demanding in its scope and less precisely defined. In anything less than an efficient totalitarian state it is also less easily available. It is not surprising then that the formal economic models of the analytical kind that are most often employed tend to be derived from those originally used at the resource level and do not usually go beyond the primary level of fishermen's costs and profits (Schaefer 1957).

One of the main kinds of difficulties that the numerical economist has to face can be demonstrated by reference to an attitude displayed by some herring fishermen in 1976 in the Bay of Fundy, when for the first time, the opportunity of "over the side" sales to foreign vessels at a premium price to the fishermen was made available. On several occasions, given an option of selling a particular catch to the foreign vessels or landing the fish at a Canadian plant at significantly lower prices, the catch was landed in Canada. As it was the objective of a major government sponsored project to increase the catch value to the fishermen, subjected to an intense cost-price squeeze, this decision was inexplicable to one of the organizers of the scheme. To the individual fisherman, the explanation for his decision was eminently rational. He knew that the particular Canadian market would still exist in 1977 but could not be sure that the foreign boats would be coming back. Faced with a choice whose outcome would be widely and publically known within the industry, he chose the Canadian plant. The assumption of optimization of profit, the basis of economic models, would not have predicted this as an outcome. Moreover, a full explanation of the reason for the choice would involve a detailed analysis of the history of the fishery and of the social and political attitudes of interest groups within it, of current policies relevant to conflicts of interest at both national and international levels, the current market situation, etc. When all this was properly dealt with, there is still the question of individual choice by people of notoriously independent attitudes. Analysis could not pretend to predict the decision that was made even in a statistical model. It might account for the actual decision after the fact.

Limits to the Relevance of the Modelling Process

There are more fundamental reasons why the potential for the analytical modelling of fisheries is severely limited. These are related to the mechanics of the decision making process at each of the levels; the extent to which the authority to make decisions is concentrated, the ability to ensure that a decision is binding on the interest groups involved, and so on. This is usually a function of the political system and this can be illustrated by referring to the Canadian Federal system. It becomes immediately obvious, on inspection of the 4 questions listed above, that authoritative decisions can be made, even in principle, only at the level of the biological resource. At the higher levels, there are political, legal, institutional, and other restraints that do not allow direct intervention to control and determine events. Instead, reliance is placed on incentive or disincentive, the creation of aims common to interested parties or other persuasive tactics. At the third and fourth level, both as optimization and allocation problems, the questions tend to become aims whose achievement results from the mobilization of effort within the system as a whole. For example the following quotation, from a Ministerial speech made in March 1980 at a meeting of the United Maritime Fishermen at Moncton, N.B., represents a policy statement with the clearest implications:

> "The allocation of fish must come from a mixture of reasons: not just what is "economical" but also the survival of communities, the preservation of a way of life, the needs of the market place, the reasonable well-being of fishermen and plant workers, and so on."

The Historical Perspective

What happens in the next 10 years will establish a pattern that will determine and constrain developments that will affect the future of almost the whole of eastern Canada. No other part of the country is as sensitive to the need for good fisheries management. It is important, then, to appreciate how we arrived at the current position so that we can discriminate between constraint and opportunity. "Those who do not study history are forced to repeat it" is a more accurate comment than "history is bunk".

And, to emphasize the main characteristic of the current situation, I may quote from Ophuls' (1977) book, *Ecology and the Politics of Scarcity*, p. 8:

> "The habitual condition of civilized man is one of scarcity. Goods have never been available in such abundance as to exhaust men's wants."
>
> "The institution of Government, whether it takes the form of primitive taboo or parliamentary democracy therefore has its origins in the necessity to distribute scarce resources in an orderly fashion."[1]

The first quotation applies with particular force to the fisheries situation because fish move freely in a 3-dimensional continuum that surrounds all of the continents. By the same token the crossing of administrative borders creates problems that increase exponentially with the number of borders crossed. Witness the management scene in European waters (Korringa 1978)!

The Development of the Resource Problem

It can easily be demonstrated that "official" fisheries biology, especially in eastern Canada, has been directed towards obtaining acceptance of a very simple biological thesis.

Fish as a renewable resource is not unlimited in abundance. This thesis can be erected into a Fundamental Law of Availability.[2] "As long as the world remains civilized it will always be technically possible to take more fish from the sea than is either desirable or advisable." The corollary of this law ought then to be: "pressure will *always* develop to encourage overexploitation." It could be said that the essence of sound management is to prevent this expectation from being realized; sophisticated management absorbs pressure rather than reacts to it.

In the northwest Atlantic the FLA was finally accepted, or at least was paid lip service by "foreign" fishing interests, in the 1970's. This happened because Canada and the United States of America could argue jointly and persuasively from the privileged position of neighboring coastal states united in a common cause. The forum in which the drama was played out, ICNAF,[3] was an international one, especially designed to achieve this goal. But the same lesson has to be reinforced nationally if we are to benefit fully from the jurisdictional vantage point we now enjoy.

There is neither space nor reason to review 1,000 years of history in detail and I will, instead, list a series of statements that conveniently brings us up to the twentieth century (see McFarland 1911 for an excellent treatment).

(1) Fisheries have been the subject of international controversy for 1,000 years or more but, until recently, not at the resource level.

(2) The initial colonization of eastern North America and the exploitation of the northwest Atlantic fisheries were very closely inter-related.

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[1] It will be noted that he says "orderly" and not "equitable."

[2] In the Age of Acronym (AA) this becomes FLA.

[3] International Convention for the Northwest Atlantic Fisheries—now replaced by NAFO, Northwest Atlantic Fisheries Organization.

(3) The current social structure of Newfoundland still reflects the events of the period when European "English" fishery interests were determined to prevent local colonizers from competing successfully to exploit the rich Grand Banks fisheries.

(4) The New England fishermen in the first half of the 18th century (and by their direct intervention) helped create eastern Canada and Nova Scotia as we know it today. This was because they wished to protect their fishing interests threatened by Continental (and pre-revolutionary) France.

(5) The American Revolution - or War of Independence - was caused largely by the almost catastrophic economic effect the Sugar Act of 1764 had on the New England fish trade to the West Indies, on which their economic base largely depended.

Despite all this, the question was not primarily a *resource* one. Some individual whale stocks and other marine mammal stocks had been decimated in some areas, but "finfish" stocks were not depleted. Indeed, as recently as 1883, Thomas Henry Huxley, Darwin's Champion, who was reporting on fisheries for the British Government, could be quoted[4] as saying:

> "The cod fishery, the herring fishery, the pilchard fishery, the mackerel fishery, and probably all of the great sea fisheries are inexhaustible. Nothing we can do can seriously affect the numbers of fish. Any attempt to regulate these fisheries seems consequently to be useless."

He was wrong, of course, but why did he say it? And why was he wrong? He said it because finfish tend to produce large numbers of eggs; from thousands for a large salmon, tens of thousands for large herring, hundreds of thousands for a large mackerel or haddock, a million or so for a large cod, 5 to 10 million for a large tuna and hundreds of millions for a large sunfish. He thought this large, even enormous, investment in reproduction conferred immunity from man on fish populations. It does not. Fish do not produce large numbers of eggs for man's benefit but for their own, and extinct herring fisheries provide mute evidence that this is so.

So that is was not until the 20th century that any real note of caution was sounded and incorporated into an instrument designed to achieve specific resource-oriented aims.

The Twentieth Century Fishing Treaties

On October 21, 1924, Canada and the United States ratified a treaty for the preservation of the halibut fishery of the northern Pacific Ocean, including the Bering Sea (Babcock et al. 1931). This treaty was remarkable in 2 ways. The fishery had begun about 1890 but for the first 35 years or so of its existence it had undergone a period of uncontrolled expansion. As with most renewable natural resources at that time, development and exploitation were the prime aims, and expectations were limited by market demands only; the conservation concept was almost unknown (Bell 1970). However, at about the time of the First World War, the continued expansion of the fishery to new grounds failed to maintain the annual yields that had been previously enjoyed. Prolonged negotiations followed between the United States and Great Britain and the resulting treaty had the honor of being the first entered into by Canada as a nation. For in the meantime, and as a result of her exertions during the First World War, Canada's sovereignty was extended to include authority to act independently in external affairs. It was, in addition, the first treaty that had as its objective the conservation of a high seas fishery that appeared threatened. The relevant portion of the text can be quoted:

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[4] See Graham (1943). *The Fish Gate*. Faber and Faber Ltd., London, p. 109.

> "The commission shall make a thorough investigation into the life history of the Pacific halibut, and such investigation shall be undertaken as soon as practicable. The commission shall report the results of its investigation to the two Governments and shall make recommendations as to the regulation of the halibut fishery of the North Pacific Ocean, including the Bering Sea, which may seem desirable for its preservation and development." (Babcock et al. 1931, p. 7)

The commission referred to was the International Fisheries Commission, created under the terms of Northern Pacific Halibut Treaty. The Treaty or Convention was revised 3 times, the last time being 1953 when the Commission was renamed as the International Pacific Halibut Commission (Bell 1970).

However, you will note that the original Convention did *not* mention anything that implied a specific quantitative or "scientific" aim; no term such as maximum sustained yield was used. This was not mentioned until the 1953 revision of the treaty, and by then a lot had happened.

The Twentieth Century Fisheries Theory

It is now recognized that much of modern quantitative fisheries theory was anticipated by the Russian scientist Baranov in pre-revolutionary Russia (Baranov 1918; Larkin 1977; Ricker 1940). However, to trace the *effective* history of fisheries theory, we must look to developments that began in the 1920's by an American economist, Pearl (Pearl & Reed 1923). He had been studying the history of the development of industry and of population demographic changes associated with it. Pearl found that increases in human population size over a period tended to follow a flat S-shaped Sigmoid curve.

The particular kind of quantitative analysis to which this led, entered fisheries biology by the back door. In fact, it is probably more correct to say via the brewery, because it was next heard of in connection with a study of increases in cell numbers of laboratory populations of Brewer's Yeast, *Saccharomyces cerevisiae* (Klem 1933). These were produced by the Frydenlund Brewery in Oslo for a student of Professor Johan Hjort, a famous name in 20th century fisheries biology. It was Hjort who realized that a very suggestive model was at hand to develop badly needed quantitative theories to answer a question he himself had formulated:

How can we determine"the relation between the toll levied by man on a given stock of animals and the capacity for renewal shown by that stock" (Hjort et al. 1933)?

His model was built up by considering a hypothetical closed area of sea, suitable for supporting whales but without any present. A few are introduced, being careful to ensure that there is at least one of each sex; these increase in number as time goes on until a certain number is reached that represents a limiting population level, the saturation level for that enclosed area of sea. The rate of increase in numbers, he maintained, would follow the same pattern with time as had been found for enclosed flasks with limited nutrients into which yeast cells had been introduced.

The argument was: At first, because the number of animals is very low, the rate of increase is very low; at equilibrium, because the environment is saturated, the rate of increase is zero. In between the rate of increase rises to a maximum and then declines. And here is the important mental switch; the idea that Hjort, in 1933, had, and what Graham, in 1939, claimed was "a remarkable piece of insight" (Graham 1939).

The rate of increase under these hypothetical conditions can be equated to the equilibrium yield from the population, in this case, of fishes. Animals cannot be removed without depressing the population size. At environmental saturation (the "virgin-stock" state), removal of animals at any given rate will take you down the curve to a population size at which the rate of increase and the rate of withdrawal are equal. This is an equilibrium yield, and there is one unique point which defines an equilibrium yield that is a maximum. This is the origin of the *Maximum Sustained Yield* concept. This aspect of the model was developed by Michael Graham and Figure 1 is taken from his 1939 paper.

Graham made a very significant change, instead of numbers he used weight as his population criterion. This is more appropriate as weight of yield is the main economic aim of fisheries. He also derived a maximum equilibrium yield, which could be properly called a "Maximum Sustained Yield" which on the assumptions of the model, can be defined quantitatively as to the population size at which it occurs. This is 50% of the original population size. As in the simplest case the catch for a given unit of fishing effort is proportional to the population size, the point at which the catch rate has declined to half the original catch rate is the MSY point.

This kind of model has since been called the "Biomass Model," treating the population as a single unit of weight, or the "Logistic Model" because it was found that the mathematics had already been worked out in the 19th century under that name. It represents one of the 2 main types of fisheries models that are in use and was first applied successfully to analyze a tuna fishery in the 1950's by Schaefer (1954). It has since been modified and generalized and the generalized version is called the General Production Model (Pella & Tomlinson 1969). However, the Generalized Production Model does not have a single, unique MSY but a whole family of them. Far too much of a good thing some people might say!

As another point of interest, neither Hjort nor Graham refer to Maximum Sustainable Yield. They both talk of an optimum yield or, more exactly, optimum catch. Hjort says, "Here, then, there is every possibility for an intelligent community to create an industry based upon an optimum catch" (Hjort et al. 1933), the phrase also used by Graham. But Graham was also very much aware of the other aspects of management with which I began this paper. I quote him directly, "No means whatever can bring permanent profit to the industry unless the rate of fishing can be controlled" (Graham 1939). "Only temporary prosperity can be expected until there is some international arrangement to prevent the rate of fishing increase" (Graham 1939).

He was, at the time, referring to an international situation centering on the North Sea Fisheries but, meanwhile, thousands of miles away, something had happened that was to lead to what we see now as modern fisheries management in this part of the world.

The North American Scene

In the early 1930's and off the west coast of North America, a Japanese fishing vessel was sighted. This is the very area of the only international fisheries convention that existed, the I.P.H.C. Convention area. This was the first of the "Distant Water Fleets" to come fishing off the North American coast. It stimulated tripartite discussions between the United States, Canada, and the United Kingdom, all of whom had an interest in developing an international body that would control fishing. It is a rather odd fact and one to ponder over that although ICES[5], an European-based scientific body concerned with fisheries biology, had been in existence in Europe for 30 years or more, it was not then in any way concerned with management functions. Management was not even considered until 1959 when NEAFC[6] was formed.

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[5] International Council for the Exploration of the Sea — founded in 1904.

[6] North East Atlantic Fisheries Convention

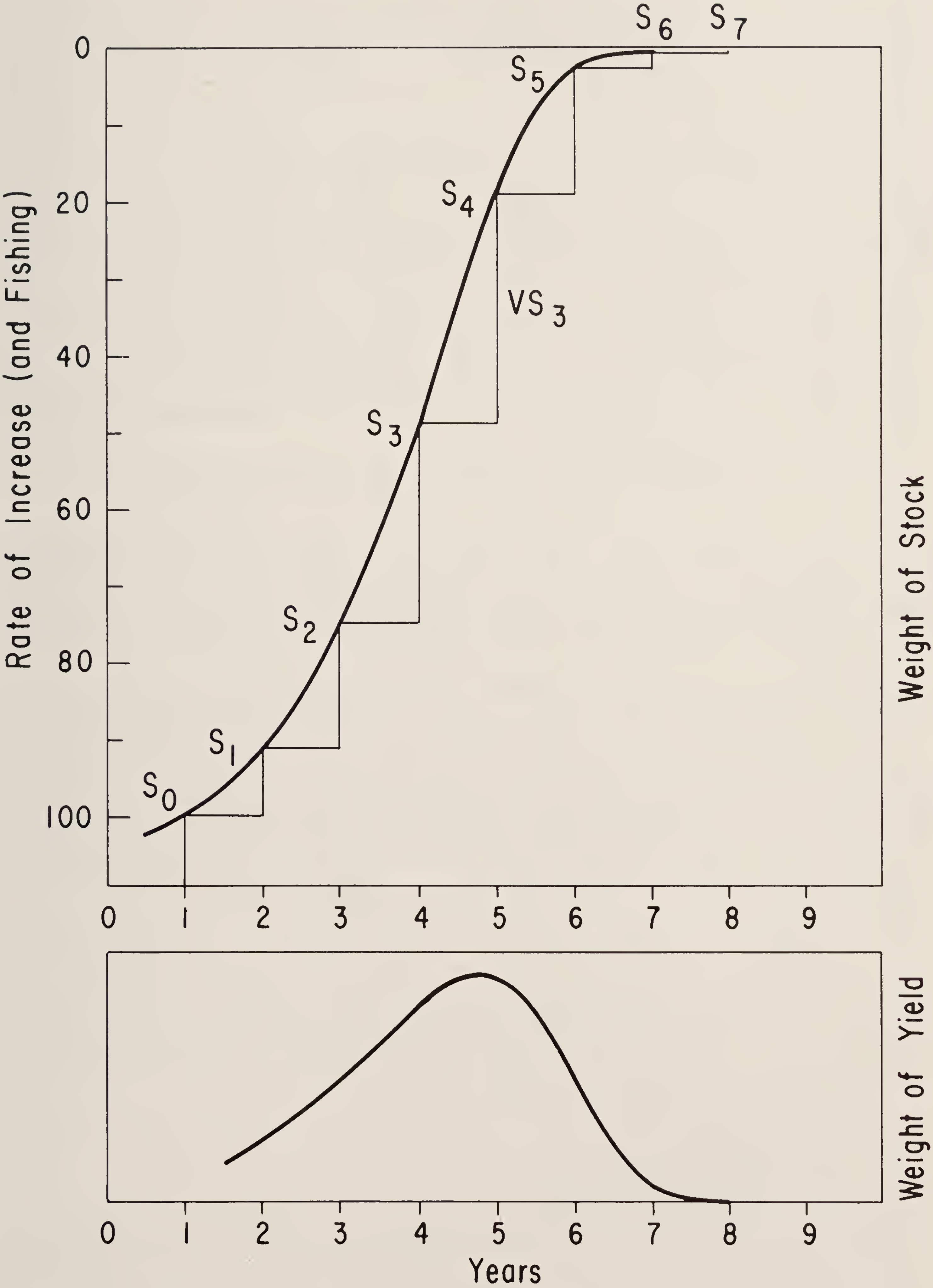

Fig 1. Graphical derivation of an S-shaped curve. (Graham 1939, p. 18)

The Formation of ICNAF

Negotiations were halted by the war but, as early as 1943, a meeting was held in London, England, between the 3 countries, to which Dr. A.W.H. Needler, a famous name in Canadian fisheries, was conveyed in a bomber being ferried across the Atlantic. This is a remarkable demonstration of how seriously the matter was being considered.

It would seem that, whereas the United Kingdom wished for an international fisheries convention with the broadest possible global approach, the United States was anxious to restrict it to the North Atlantic and to include an area off the east coast of the United States, in the general Gulf of Maine area particularly, where its traditional historical interests were concentrated. Canada blandly took the view that she would sign anything, and this, it would seem, stimulated the United States to sponsor a Convention and do all the work in its preparation as soon as possible. The Convention was ready by 1949, and was signed on February of that year at an inaugural meeting attended by 11 countries. It came into force on 3 July 1950 when the fourth of the original signatories had ratified the agreement in their parliaments. This method of activation was written into the Convention and Canada was, in fact, the fourth to ratify. And hereby hangs a tale.

The original signatories on 8 February 1949 included both Canada and, separately, "His Majesty's Government in the UK and the Government of Newfoundland in respect of Newfoundland." The ratifying Government, however, as listed in the Convention itself, was "Canada (including Newfoundland)." Newfoundland had joined the Federation in the meantime and, indeed, this was the first treaty signed by Canada as an entity which included Newfoundland. The important point is that the 4 founder members enjoyed certain privileges that later signatories did not have.

The area covered by the Convention was carefully defined and divided into 5 subareas, each of which was a management unit under its own "Panel." To be a member of a Panel and thus to initiate and influence management divisions, you had to have a substantial fishery in the subarea *unless* you were a founder member. Canada qualified as a member of Panel 5 because she was a founder member even though she had no substantial fishery in the important Subarea 5, which included the Gulf of Maine and Georges Bank. Canada and the United States could thus operate jointly over the whole Convention area. A stroke of luck. Or was it?!

The ICNAF Convention had another distinction. It was the first fisheries convention to spell out its management objectives and the means by which they were to be met. This was set out in the famous Article VIII on Regulatory Measures. The Commission, through its member governments, could recommend certain measures designed to keep "the stocks of those species of fish which support international fisheries in the Convention area at a level permitting the maximum sustained catch." The measures were (Anon. 1969):

(a) by open and closed seasons
(b) by closing certain areas
(c) by establishing size limits
(d) by prohibiting kinds of gear
(e) by establishing quotas

And, a most important point, the recommendations had to be made, specified clearly in the text of the convention, "on the basis of scientific investigations" (Anon. 1969). It became obvious in the work of the Commission that this meant *only* on the basis of scientific investigations. No social, political, or economic factors could affect or influence the advice presented by the scientists.

But this is the first mention of the term "maximum sustained catch."[7] It was not introduced with capitals as, for example "Maximum Sustained Catch," and was not defined anywhere in the Convention. The regulatory measures were "designed to keep the stocks of those species of fish which support international fisheries at a level permitting the maximum sustained catch"; no implications that single species management was obligatory. These points need to be stressed because of the enormous quantities of paper that have been used up in the discussion, analysis, and criticism of the Maximum Sustained Yield (MSY) as a management objective. A full treatment of the MSY debate at this time would be inappropriate, but it is worth pointing out that most of those pontificating about the advisability of revising management aims to avoid reliance on MSY have had very little first-hand experience in the management of complex international fisheries, such as those of the east coast, or knowledge of the efforts being made to conserve and develop them for the benefit of Canadians (and Americans one must add!). And without these efforts, the management of our fishery resources as we now know it would not have been possible.

But to deal specifically with the question of the management aims of ICNAF in relation to "MSY" or msc, it is necessary to go back to the 1930's.

Analytical Models

The logistic model, or the sigmoid curve model, was not the only kind of model being investigated, even in the 1930's. As early as 1931 E.S. Russell was examining the question from another point of view (Russell 1931). He considered a completely self-contained stock of fish of one particular kind which is being fished by a standardized gear that catches fish only when they have reached a particular length. This divides the stock into 2 groups which were called the "catchable stock" and the "non-catchable stock."

A catchable stock has, for example, an initial total weight of S, at the beginning of a year; during the year it will be joined by "recruits" that have reached the catchable size. Also, the individuals in the catchable stock will grow. Both these factors increase the stock size. During the year, fish will die from various causes and some will be caught.

We thus have a balance sheet and a means of following changes in the catchable stock.

$$S_2 = S_1 + (A + G) - (C + M)$$

where:

S_1 is the weight of catchable stock at the beginning of the year
S_2 is the weight of the catchable stock at the end of the year
A is the weight of recruits joining the stock during the year
G is the growth of all (surviving) individuals of the catchable stocks for the year
C is the weight of the catch for the year
M is the weight of all fish dying from natural causes during the year

Of course, all that this does is to simplify the picture to the degree that it becomes manageable mathematically. It is something that biologists, working in a difficult subject, often have to do for the benefit of mathematicians, physicists, and chemists who are working in the "easy" sciences.

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[7] Item 1 of Article VIII of the ICNAF Convention states: "The Commission may, on the recommendations of one or more Panels, and on the basis of scientific investigations, transmit to the Depositary Government proposals for joint action by the Contracting Governments, designed to keep the stocks of those species of fish which support international fisheries in the Convention area at a level permitting the maximum sustained catch by the application, with respect to such species of fish, of one or more of the following measures . . . ." (Anon. 1969).

It remained to express the rates of the various separate factors in appropriate form and the Beverton and Holt model (Beverton & Holt 1957) is as convenient as any to follow because of 3 things which they did.

Firstly, they *excluded* recruitment in their basic model because it was obvious that the number of fish surviving each year, out of billions of eggs produced by any reasonable sized stock, varies, apparently in an unpredictable way. This was found to be true for almost every stock and species studied. They expressed their results in terms of the individual recruit, the average fish-in-the-sea. The term "Yield Per Recruit" should be familiar to anyone having nodding acquaintance with fisheries. Secondly, they distinguished between a length at which fish entered the fishing area and the length at which they would be liable to be caught. This latter depended on the mesh size used in the cod-end of trawls, the trawl fisheries being the most important considered. This allowed them to use the model to study the effects of varying the mesh size, of controlling the size at which fish are first captured.

Thirdly, they chose a model for fish growth, already available, that gave an expression for growth and mortality in a simple mathematical form. Eventually, though not to begin with, this led to some very nice simple relationships. The model essentially balances growth and mortality and can be simply illustrated as in Figure 2. For explanatory purposes, we consider a number of individuals of a single years spawning, a "brood" or "year-class", of a stock of a species of fish at an early life history stage that is subject to a steady mortality drain from natural causes. This "natural mortality" results in an exponential decline in numbers. However, each individual is increasing in weight, and in a broadly sigmoid pattern with time. This means that the total weight of the year-class, the biomass, changes with time. A little thought should show that the biomass of a year-class must increase to a maximum and then decline, eventually to zero. The shape of the biomass curve with time will depend on the shapes of the mortality and growth curves. But as long as the numbers are large and size small to begin with, then the total weight of a year-class over the life history will rise to a maximum and then decrease.[8] If we were considering an aquaculture operation and the year-class was a batch of young all introduced into the pond at the same time, the maximum biomass point would be the ideal point to drain the pond and harvest the total crop, if maximum yield was the object.

The Analytical Maximum Sustained Yield

The situation with natural populations is different. If it is possible to selectively catch fish at the size associated with the biomass maximum, it becomes conceivable, in principle, to get the maximum yield from year-classes. A trawl net of suitable mesh size could be chosen to select the size, but to crop all fish as they reach that size would demand an infinitely high *rate* of removal—of fishing effort. This is impracticable, and the pioneer workers, like Russell, Hjort, and Graham were aware of it. Ricker also, appreciated this argument and worked out a way to calculate a size of fish smaller than this critical size, and thus to achieve an optimal catch level at a more realistic degree of effort (Ricker 1945).

The fact remains, however, that it is the biomass maximum that, in the Beverton and Holt model, best corresponds to the ideal concept of Maximum Sustained Yield. As far as I am aware, this point has never been made in discussing the concept. Nor is it at all well known that the formula defining this maximum, in terms of the length at capture that corresponds to it, was worked out by Beverton and Holt (Holt 1958; Beverton & Holt 1966) and remains one of the simplest and neatest formulas in fisheries biology. The length is referred to as the Critical Length and is defined:

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[8] This will be so long as the average weight of the ripe female gonad is less than twice the total weight of the female.

$$\text{Critical Length} = L\infty \times \frac{3}{3 + M/K}$$

Here, L∞ is a measure of the limiting (maximum) size of the fish concerned, M measures the mortality rate and K, the growth rate. If, in suitably scaled units, M and K are equal, the critical length is 75% of the limiting length.

As an "ideal" standard this Critical Length has much to commend it.

Three yield curves are depicted in Figure 3. Each of these yield curves represent the equilibrium yield at a given length at capture and over a range of different levels of sustained effort. For each length at first capture there is a maximum sustained yield which, for any length equal to or greater than the Critical Length, is approached asymptotically. Below the Critical Length the maxima are reached at intermediate levels of effort.

Figure 3 has great pedagogic value but, as must be pointed out, the model was not available at the time of the drafting of the Convention and the objective "maximum sustained catch" was not defined. Indeed, I am doubtful whether the people draft-

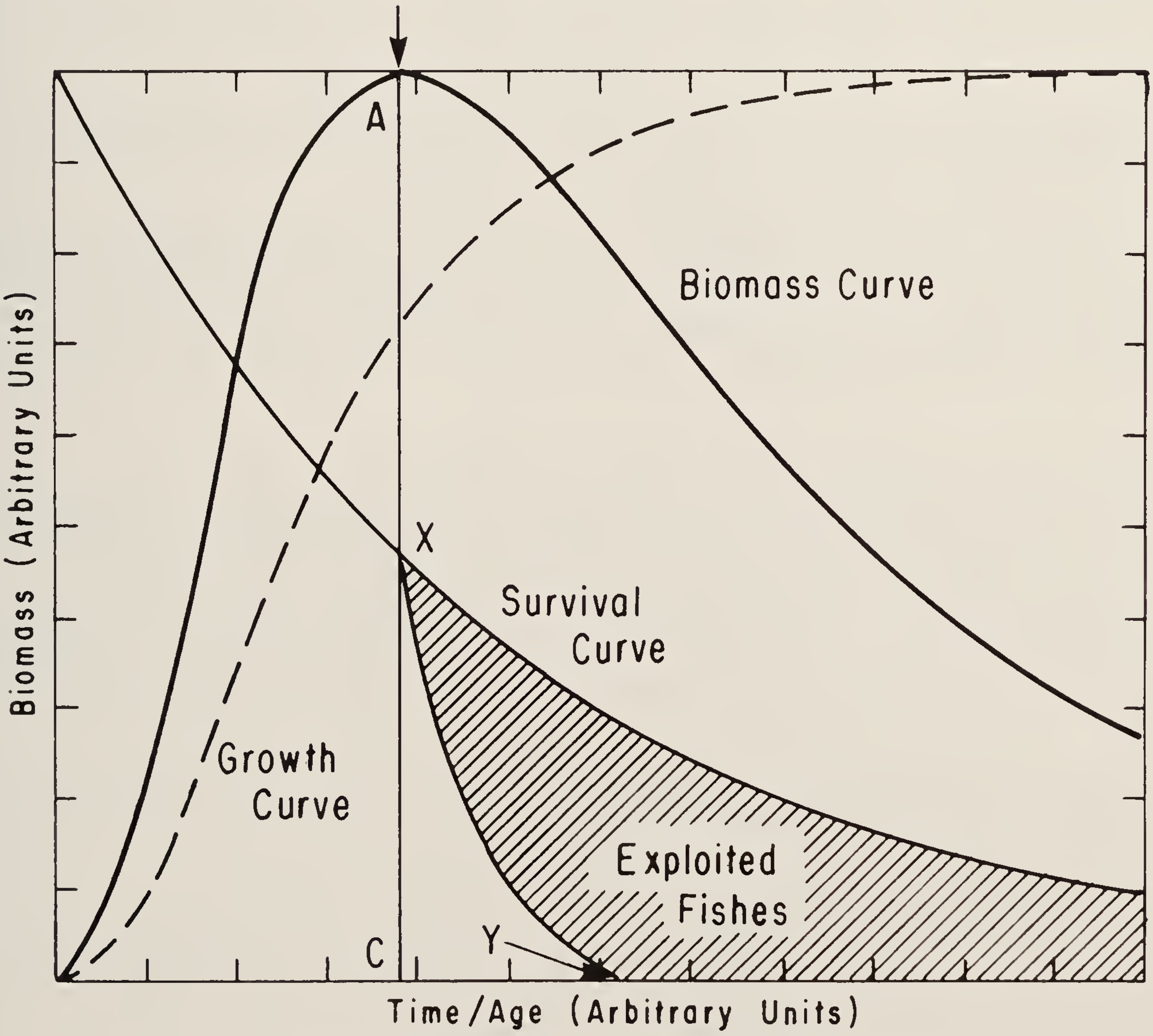

Fig 2. Model for an exploited fish population. The point of maximum biomass, A, corresponds to a particular size—and a particular age, C. At this point increase in biomass resulting from growth equal losses from mortality. The maximum possible yield would be achieved if instantaneous cropping began at X and no fishes survived beyond this point. In practise a finite fishing effort generates a new survival curve, XY, between the original survival curve and the axis XC. (Fryer & Iles 1972, p. 426)

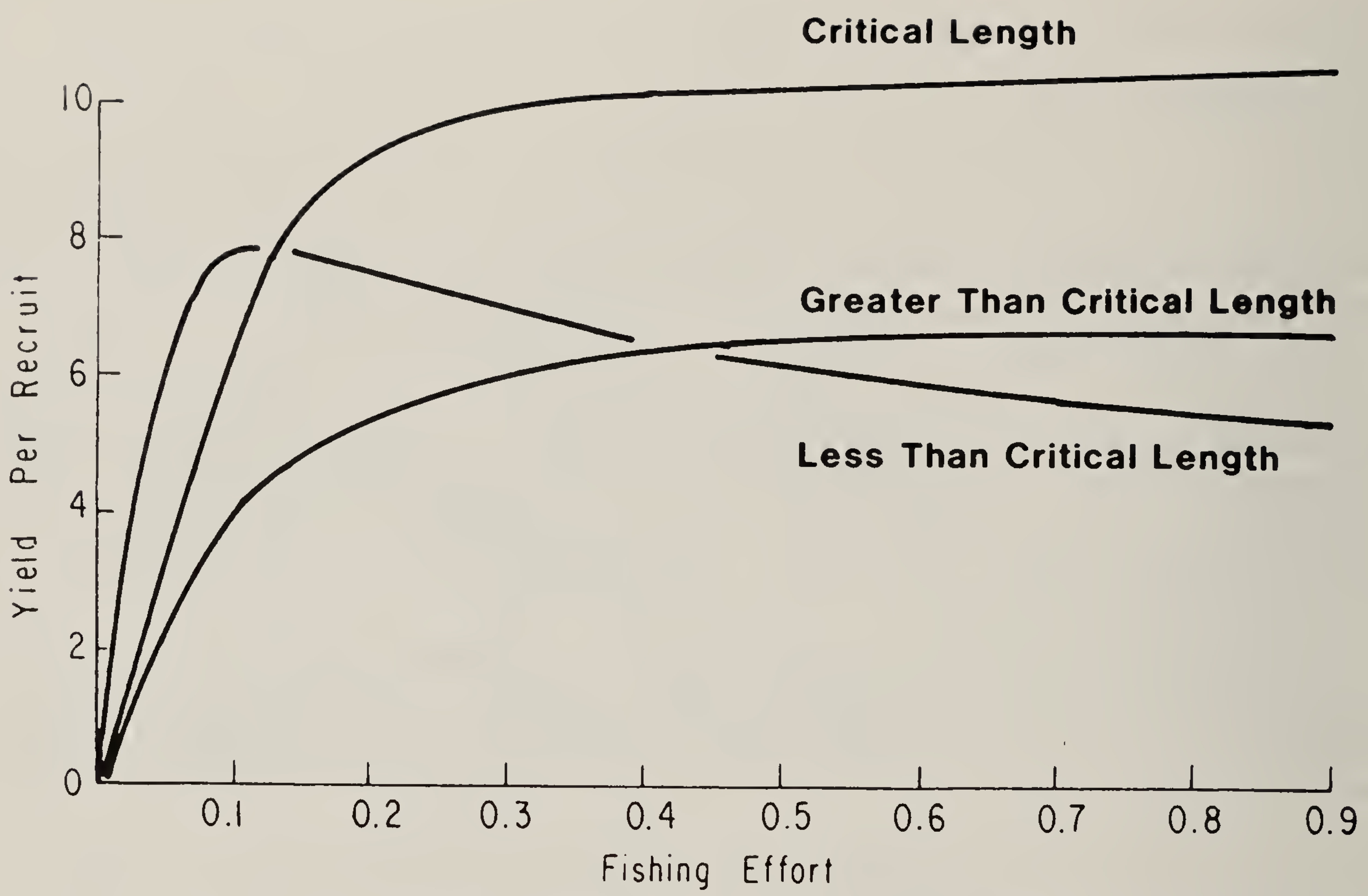

Fig 3. Yield per recruit curves at different lengths-at-first-capture relative to the critical length: Beverton and Holt (1957) model.

ing the Convention had anything specific in mind. As did both Graham and Hjort, they could well have used, instead, the term "optimum" in the sense that it represented a "best" under the circumstances.[9] And, in fact, it was not too long before any argument became academic.

The Extension of Jurisdiction and ICNAF in the 1970's

In 1970, Canada and the United States concluded an Agreement on Reciprocal Fishing Privileges. On the east coast, this was concerned largely with an industry based on juvenile herring caught along the New Brunswick and Maine coasts and which, in the mid-1960's in the United States and the late 1960's in Canada, had declined substantially; by 1971 these fisheries appeared threatened by economic collapse and the factor held responsible was an upsurge of foreign fishing on adult herring.

This was an almost classic example of traditional fisheries conducted, in this case, largely within the 3-mile limit, apparently being threatened by a recently developed offshore fisheries conducted by "distant water fleets." As a test case, they provided both the reason and the opportunity for a coordinated Canada-United States attack on the wider problem of establishing control over an accelerating expansion of effort by distant water fleets in the northwest Atlantic as a whole. In the view of Canada and the United States this was threatening the fisheries of the coastal states. The Reciprocal Agreement provided an umbrella for the preparation of joint Canada - United States proposals to ICNAF to limit herring catches in the Bay of Fundy-Gulf of Maine area, and these were presented at the Annual meeting of ICNAF in June, 1971, in Halifax. They failed to gain acceptance and to explain why this was so, introduces the important question of sub-allocation.

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[9] Optimum: best; most favorable or most conductive to a given end, especially, under fixed conditions (*Websters New International Dictionary*, unabridged, Second Edition, 1960).

As described above, the ICNAF Convention, as originally drawn up in 1949, had a "regulatory" section, Article VIII,. which specified what measures could be undertaken by the Commission to achieve what aims and under what circumstance.

The relevant aim was "achieving stock levels permitting the maximum sustained catch."

The relevant circumstances was "on the basis of scientific investigations" (and it will be remembered *only* "on the basis of scientific investigations").

In its early years the Commission had not relied on catch limits as a regulatory measure but on mesh size restrictions to control the minimum size of fish.[11] This determines which yield curve would be followed (see Fig 3). It was not until the mid-1960's that a scientific report was produced for the Commission by Templeman and Gulland (1965) and which challenged the validity and the effectiveness of all 3 components of the ICNAF regulatory apparatus.

It was pointed out, firstly, that the real benefits to be gained by management were in savings in the cost of fishing rather than increased yield and, as a corollary, that "economic and technical considerations" should thus be allowed as a basis for decision making in addition to "scientific investigations." Secondly, it was demonstrated that the achievement of a Maximum Sustained Yield, and either a stable fishery or an economically efficient fishery, were incompatible. This led eventually to the substitution of "optimum utilization" for "maximum sustained catch" as a management aim. It should be noted that the phrase was "optimum utilization" not "optimum yield", and not "optimum sustained yield" either. And it should be remembered that treaties are documents in which words and phrases are very carefully weighed as to their implications. Thirdly, it was pointed out that catch limitations would not be effective unless the Total Allowable Catch[11], the "global" quota, could be suballocated, each interested group, in this case of course, each country, being given its share.

The Origin of Sub-allocation of TAC's

These points were all accepted by the Commission in 1969, but by mid-1971 the necessary changes in the Convention had not yet been ratified by the member countries and suballocation was not available as a part of the regulatory apparatus. Thus, although everyone agreed at the 1971 Annual Meeting on the seriousness of the herring situation, it was impossible to agree on an acceptable solution. This was because each of the national fisheries concerned had its own characteristic seasonal pattern, which clearly favored any country whose season occurred early in the quota year rather than another. There is an important point to be made here. Anyone proposing regulation at ICNAF in terms of any aim, or by using any method not legally part of the Convention at that time, would have been ruled out of order. No one was naive enough to do so although alternative aims, including optimum utilization, had been discussed for years.

Attempts were made to change the timing of the quota year to help solve the problem, but these were unsuccessful and, in view of the urgency of the matter, a Special Meeting of ICNAF, the first of many, was called for January 1972, in Rome, and for which scientists were called to make "extraordinary efforts" in preparation. The Commission gave the scientists 6 whole months to solve problems that had been years in the making!

By 15 December 1971, the "suballocation" change in the Convention had finally been ratified by member countries and became part of the Convention. Agreement

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[10] Incidentally, this committed them to the Beverton and Holt type model and to thinking about msc's in Beverton and Holt terms but, in fact, nobody raised the issue as to what msc meant.

[11] The origin of the famous "TAC" concept.

was reached in January 1972 at the Special Meeting in Rome for the 3 major herring stocks in the Bay of Fundy-Gulf of Maine-Georges Bank area. The ability to suballocate was, of course, the key factor allowing this. What is not fully appreciated is that this agreement became possible only because of the amendment to the Convention which removed "scientific investigations" as the sole basis for advice and decision making. There *can* be a scientifically based justification for recommending setting an overall catch limitation; the division of a quota or TAC, however, cannot be based solely or indeed, at all, on *scientific* criteria. Science and the scientist were put in their proper place in the management scheme, and I do not imply that this is any way an inferior position. Indeed, it meant that the advice that scientists had been giving for years in the interests of the safeguarding of the resource, was finally acted on. An essential flexibility of action was introduced to translate advice into administrative action.

I will not follow subsequent events at ICNAF, interesting as they were. Instead, I will consider the problems Canada was faced with in handling its own suballocation.

The Myths of Common Economic Goals and the Maximum Net Economic Yield

It is one more of the interesting paradoxes we see in the recent history of international management is that the inclusion of "technical" and "economicl" considerations as grounds for action, and the way that this then allowed suballocation as a means to achieve control over fishing effort, also ensured inevitably that ICNAF could not pursue common economic goals. Once a country had been allocated a share, it was free to do whatever it chose with it; the argument in negotiation centered on just how big was the allocation. The fundamental differences in political and economic systems amongst the ICNAF countries made the pursuit of a common economic aim impossible, and suballocation, once agreed on, removed the problem of trying to define and establish one.

Again, there was nothing new in this. In 1957 Schaefer had discussed this very point in dealing with the Maximum Net Economic Yield as an alternative approach to Maximum Sustained Yield as a management aim (Schaefer 1957). His argument is worth summarizing and commenting on.

He first maintained that MSY (he referred to the "logistic" MSY) is a property of the population and not the exploiter and, as such, is a (fixed) function of the biology and ecology. This "quasi-absolute" nature of physical yield, incidentally, is a highly desirable feature as a management aim under certain conditions, where for example conflict of interest is such as to demand a "neutral" criterion to set limits within which conflict must operate.

The Maximum Net Economic Yield, MNEY (estimated, it must be stressed, only for the primary sector, the fishermen), on the contrary, depends on the value of and the cost of catching the fish. This varies from country to country.

It is therefore impossible to establish a unique relationship between MNEY and fishing effort and, because of this, to reach agreement or a level of fishing effort based on MNEY in an international high-seas fishery. MNEY is therefore an impossible basis for joint management among nations. It is no easier to rely on within a democratic society, it may be added.

For, within a country, different interested groups have access to the same political and economic system and the quantitative resolution of conflicts of interests which, incidentally, is one of the best pithy definitions of management I know of, has to be done under a very different set of rules which are far less structured and far more equivocal than is so for an international treaty such as the ICNAF Treaty. This dumping of the management problems in the individual country's lap has been referred to as "internalization". This happened with the Canadian fisheries when the program initiated and carried through via ICNAF led to Canada's extension of management control to 200 miles in 1977.

The Canadian Problem

Both biologically and socially, politically and economically the Canadian east coast fisheries form a very complex system with actual and potential conflicts of interest that defy complete analysis. You cannot model these fisheries.

It is worthwhile at this point to emphasize a principle of some significance. No major change in any fishery that results from a management decision (or indeed from any environmental change) can affect all interested parties equally. In the international arena this principle was invoked in another way as the Principle of Equal Sacrifice. No change was acceptable to a country if it was affected adversely to a greater degree than another. The criterion for measuring degree was flexible and it is inevitable that any regulatory change must be differential in *some* way. In international fisheries debates, it allowed a vehement support of the need for resource protection, while at the same time, there could be an expression of heartfelt regret that no practical solution is emerging which satisfies the sound democratic principle of equality of sacrifice. The man in the middle, the scientist, whose advice is the basis for any decision on resource removal is, naturally, held responsible for closing the door to the only commonly accepted solution, the increase in allowable catch that would solve everybody's problems.

The Sanctity of TAC's

One of the most significant of all management developments, occurred at the 1973 Annual Meeting of ICNAF in Copenhagen (Anon. 1973). Eric Gillette had been appointed chairman of Panel 3 to replace the unexpectedly unavailable regular chairman. An experienced negotiator with Trades Unions in the United Kingdom, he was skilled in procedural matters. At a crucial stage of a discussion on the allocation of national shares of a TAC and after the usual plea by each country's delegate that their requirements could be met quite easily by an (insignificant)[12] increase in the TAC, he proposed a motion from the chair. This motion was to the effect that any proposal as to allocation of quota shares that involved increasing the TAC should be ruled out of order by the Chairman. Nobody could object to this without appearing to be careless of the accepted need for conservation, and a practical convention became established at ICNAF that simplified matters and led to greatly increased efficiency in decision making.

This also had the effect of removing the scientist one stage from the controversial aspects of *who* gets the fish, a separation of roles between the scientist (as a scientist) and the manager that many people see as essential to his proper function (e.g., Gulland 1977). It also emphasizes a crucial value of TAC setting in an overall management process. A fishing enterprise in an allocation system is usually interested in how much fish of a particular species it can count on being able to catch. The captain of a Bay of Fundy herring purse seiner wants to know what is his allocation for the season, and the purse seine fleet, what its total allocation is compared, say, with that of the gillnet fleet. The 1980 purse seine allocation of 44,000 MT is still 44,000 MT whether it is allocated from an MSY, an MSC, an OSY, an MNEY, a pre-emptive quota, a by-catch from a silver hake fishery, or an allocation from a global estimate based on all finfish species in the Bay of Fundy Management Area on a Bio-Energetic Multi-Species Ecosystem Dynamics (BEMUSED) basis.

Within Canada a management system is being put together which is capable of dealing with these "internalized" problems and which takes into account the realities of the Canadian fishing scene. What is seen as an essential separation of "scientific" and "managerial" input takes place at the presentation of advice on a catch level. It is difficult to conceive of any other kind of system that might be developed. As it is, any improvement in the scientific basis can be incorporated without disrupting the system as a whole.

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[12] The proposed increase was usually not large enough to exceed the upper limit of the scientists' estimates of allowable catch!

No matter what general basis for management is agreed upon, or sanctified as a desirable or essential aim, its translation into effective management action has to consider both the conflicts of interests themselves and the way in which the groups holding specific interests can influence the decision making process at the higher level of questioning introduced early in this paper.

Nor is it possible to ignore the "historical load", the natural resistance to the major changes in the status quo that many suggested alternative systems imply, but whose proponents do not usually openly recognize. How do we get to the new system from where we are?

Within the Canadian management regime the fishery biologist has to go on playing exactly the same role as he always did: objectively trying to answer the resource question stated by Hjort, "How do we determine the relation between the toll levied by man on a given stock of fish and the capacity for renewal of that stock?" There is one major difference between then and now. Then—as we were working to help Canada establish management control and prime access to the resource by getting rid of the foreigners—we were heroes. Now, we are liable to be blamed for the state of the resource as if we caused it and not merely assessed it. It is unfortunate, but true, that Canadian fishing effort, unless controlled and limited, can have as deleterious an effect on fish stocks as did an equivalent amount of foreign effort. This fact of life has not yet been fully assimilated, and because of this, and to finish on a plea, the scientist is more to be pitied than to be blamed.

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FUNDAMENTAL ISSUES FACING THE CANADIAN FISHING INDUSTRY IN THE 1980's

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The 1970's have seen significant changes in the structure of the fishing industry in Canada. It has brought opportunity and problems. The 1980's will be no different in that the changes will be at least as great if not greater and will bring a major challenge. As in most areas of research, the more that is investigated and answered, the more questions that are uncovered. The 1980's brings us the challenge of improving our knowledge of the species and of the technology of harvesting and marketing.

Introduction

In this paper I attempt to give an insight into some major issues facing the Atlantic fisheries and areas of research and technological development as seen through the eyes of the fishing industry. It is necessary to mention that the views which I present are my personal views and are not necessarily supported by either of the companies for which I work or the industry I represent.

The subject matter of this paper is divided into 3 parts. The first section is a brief presentation of what the immediate past decade has brought to the Canadian fishing industry. Hopefully, this overview will give an idea of the structure and changes which have occurred and give a better feeling of some of the more significant problems which face this renewable-resource industry. The second section is my interpretation of some major, fundamental issues facing the industry during its entry into the 1980's. The third section will point out some of the research and technological developments which the industry sees it will require in the present decade.

Changes in the Canadian Fishing Industry Between 1970 and 1979

The 70's have seen tremendous declines and growths in the Canadian fishing industry, particularly the east coast fishery with which I am most familiar. The entry into the 70's and the exit from the 70's have seen almost equal amounts of fish being caught by east coast fishermen. However, species, end-use, market areas, and value have substantially changed. Also during the 70's, a considerable dip in availability of groundfish occurred because of over-exploitation, primarily by distant water fleets from other countries. The following points illustrate the nature and the change in dimensions of the Canadian fishing industry.

Increases in Volume and Value of Fish Landed

Canada's fishery, both on east and west coasts, is a near-water fishery based on traditional species. Canada has no distant water fleet and is unlikely to develop one because of the imposition of 200 mile limits by most foreign nations. The figures shown in Table I indicate that though the 1970 and 1978 landed tonnages were similar, their value was increased by 331%, much more than the consumer product or cost of living increased during that period. Table I does not show the dip in east coast groundfish landings, to 418,000 tonnes, that occurred in 1974. The increase in value has been one of the major changes in the 70's. The costs associated with this increase in landed value have not been fully passed on to the consumer. By changes in technology and increases in product flow through the plants, costs have been kept in line. However, as we approach capacity of these plants and vessels, the cost squeeze will be felt by the processors and fishermen. This is because of requirement of additional capitalization for new plants and vessels as well as the law of diminishing return in vessel utilization. This profit squeeze has started to occur. It is noticeable, for example, in the reduced return on investment as shown in the 1979 financial returns for National Sea Products Ltd. (National Sea Products Ltd. 1980).

Significance of Exports to the Canadian Fishery

Canada presently is the largest exporter of fish in the world. This has been a significant change during the 70's. In 1970, we were in sixth place and by 1978, had increased to first place with exports of over \$1 x 10^9. This points out the importance of exports and Canada's ability to viably compete in international markets. Traditionally, our largest market has been the United States. This is still true, although export patterns have changed in the 70's. During the period 1960-1969, groundfish and fishmeal were major exports. During the 70's pelagic species such as herring, mackerel, and squid have supplied an increasingly important segment of Canada's exports, e.g., major herring exports to Europe and squid to Japan. This trade will hopefully continue into the 80's because of the economic pressure to export the excess fish products.

The 200 Mile Limit and Stock Increase

The greatest single change in fisheries in the 70's has been the introduction of the 200 mile limit, both in Canada and elsewhere. During the late 60's and early 70's, the majority of fish caught off Canada was by foreign vessels. For example, Spain and Portugal caught 620,000 tonnes of cod in the International Commission North Atlantic Fisheries (ICNAF) areas in 1968. The amount now caught is legally zero, but will probably be about 17,000 tonnes in the areas in the head and tail of the Grand Banks outside the 200 mile limit. Stocks are increasing after this over-fishing because of the removal of foreigh fishing allocations, reduced quotas, and lower fish mortality. This trend will continue in the 80's with possible substantial inroads for Canada's fleet in non-traditional species. The reduction in catch, which all the distant water fleets of the world now feel, allows for increases in exports to countries now operating such fleets, e.g., Spain, Portugal, and eastern European countries. This opportunity is now being exploited by Canadian processors.

Capital Investment in the Fishery

During the last few years, capital investment in the fishery has greatly increased. Information is difficult to obtain as it is considered proprietary and confidential by most fishing operations. Table II gives the amount of capital invested in fishing vessels and plants. Replacement value of fishing vessels can be roughly obtained by multiplying existing capital factor by 3. The reasons for such a large escalation in capital costs are the increases in size of new, versatile vessels, engine horsepower, and additional equipment. Roughly speaking, plant capitalization can be considered to be \$0.20 per pound of annual landed fish capacity.

Legal and Fiscal Activities of Government in the Fishing Industry

The 70's have been a time of tremendous increase in government regulation and control. The quota and management systems have been implemented as well as strong government regulation in licensing, catching power, and vessel replacement. Government involvement in financing has vastly increased. In 1976-1977 the Fisheries and Oceans budget was \$2.5 x 10^8, compared with \$4.3 x 10^7 in 1970-1971.

Table I. Canadian seafish landings and landed values

		1970 (Actual)	1978 (Actual)	1979 (Projected)	1985 (Projected)
Atlantic Total	Q	1,173,959	1,153,231	1,242,450	
	V	125,685	408,466	485,100	
Groundfish	Q	579,033	612,052	705,800	
	V	54,543	162,266	207,400	
Pelagic	Q	515,453	313,408	265,450	
	V	23,636	67,499	60,100	
Molluscs	Q	79,473	227,771	271,200	
	V	47,506	178,701	217,600	
Pacific Total	Q	117,021	199,183	158,750	
	V	60,255	249,729	314,400	
Groundfish	Q	32,716	32,538	36,200	
	V	12,823	25,946	31,400	
Pelagic	Q	78,648	158,154	113,150	
	V	45,810	215,745	273,100	
Molluscs	Q	5,657	8,491	9,400	
	V	1,622	8,038	9,900	
Canadian Total	Q	1,290,980	1,352,414	1,401,200	2,669,000
Sea Fisheries	V	185,940	658,195	799,500	—

Q = tonnes V = 000's $

Source: 1970—Annual Statistical Review of Canadian Fisheries, Vol. 10, Fisheries and Oceans, Ottawa
1978-1979—Tim Hsu, DFO, Personal Communication.
1985—DFO, Worldwide Marketing Study

Table II. Capital Investment in the Fishing Industry
Value in '000,000's $

		Atlantic Industry	Fresh Water Industry	Pacific Industry
Primary	'77	260[1]	65[2]	325[3]
	'78	276	69	345
Processing	'77	490*	N/A	N/A
	'78	670**		

[1] 85% vessels [2] 95% vessels [3] 95% vessels

* Estimate—Fisheries & Oceans Statistics Section
**No total available

Substantial government assistance is also available from provincial loan boards which have advanced greatly increased credits for the purchase of vessels during the last 2 years. In 1978-1979, the Nova Scotian Government, alone, lent $\$3 \times 10^7$. The Department of Regional Economic Expansion (DREE), Small Craft Harbours, the Unemployment Insurance Commission (U.I.C.), and others have all been involved in subsidizing and controlling the direction of development of the fishery.

In summary, the situation for availability of stocks looks extremely good for the 80's. The slump in the mid-70's has turned into a boom in the late 70's. Unofficial sources quote that stocks of traditional groundfish will be above the levels estimated in 1978 in government publications. The health of the inshore fishery presently looks good; however, significant over-capitalization and lack of concern over efficiency or quality will cause restrictions upon operating profit in this sector. The same may occur in the offshore fishery. The processing industry could also incur profit reductions in the 80's. This all goes along with the cyclic nature that the fishery has seemed to follow. This is all likely to continue and, in my personal viewpoint, we will be in very tight financial operating conditions for the next 3 to 4 years. It is very possible that the prices paid to fishermen will drop over the next few years as has occurred on the west coast.

Fundamental Issues for the Fishing Industry in the 1980's

The fishery is an industry based upon renewable resources. It differs from other resource industries, e.g., agriculture, forestry, or mining because the resource can only be controlled by management of the level of harvest. Hence the direction of general development of the fishery is limited not only by intangible factors of fish biology but also by legal issues arising from regulation. Below, I have outlined a number of the fundamental issues that will affect the industry in the 80's. It is not a complete list, but does provide insight into some of the factors which will control the development.

Common Property Issue

The industry is characterized by the common property aspect. In agriculture with the ownership of land, and in mining with mineral rights ownership, there is direct control over the resource, thus giving farmers and miners some ability to control production. In fishing, anybody can have access, dependent only upon government regulations in existence at the time. The total allowable catch (TAC) is available for harvesting by any individual meeting these regulations. His primary motivation is to catch more of the TAC than his neighbor; therefore his response is to increase his own fish catching power to the ultimate allowed by his financial ability and existing government regulations.

This common property aspect of fishing has led to the effort to catch more fish regardless of cost efficiencies or quality considerations. Therefore, people have replaced existing vessels with larger boats, factory freezer vessels, placed gutting machines on board, increased the horsepower of their vessels and so on—all to gain a bigger cut of the common property, at the expense of costs, labor, and fish stocks. This common property aspect will no doubt be modified in the 80's as it has in the 70's by the implementation of quotas, controls on fishing activities by controlling vessel horsepower or gear. The implementation of changing this common property aspect is a difficult one and rests primarily in the political sector. The pressure to change will no doubt come from the fisheries management sector of government. It may be asked "How can we change the common property aspect?" One suggestion has been to have boat or enterprise allocations of catch, i.e., boat quotas or percentages of the TAC which could be caught by each vessel. This would be considered to be transferrable and could be sold on a commodity or stock market basis. Thus a fisherman, or fishing company, could select the species which he wanted to harvest and the amount which would be the most suitable for his vessel or for the one which he was building. Then the effort would be to maximize profitability by increasing efficiency and quality. This would then have the effect of controlling the harvest and hopefully improving efficiency. This has been implemented to a limited degree in the Labrador shrimp fishery and the mobile herring seiner fleet. My personal reservations about these procedures are associated with the methods of implementation, the division of quotas, and the way of activating such a system.

Overcapitalization

It can be shown by economic projection, and it has been proven by experience, that substantial profits are made in virgin fisheries that are undercapitalized both in fishing and processing equipment. However, as the fishery matures, effort increases, capitalization increases, efficiencies decrease because of excess processing and fishing capacities, thus leading to drops in catch per unit effort and lower profit.

There are a number of reasons for overcapitalization, which differ from the point of view of the fishing sector and from that of the processing sector. In the fishing aspect, as shown above, the common property character of the resource leads to overcapitalization, but in addition, government regulations and subsidies exacerbate this pressure. Subsidies such as those from DREE and low interest loans such as those from the Fishermen's Loan Board increase the ease of companies and individuals to invest significantly more capital in the industry than is required. During the 1970's there has been an increase in the rate of transfer of public money into the fishery sector and this rate continues to grow with no effort to realistically control it. The government support of the increase of seasonality by weighting the inshore versus offshore balance in catching capability accentuates the problem. The issue causing the tying up of the offshore trawlers in January 1980 was because the shift in quota allocations under the Groundfish Management Plan-1980 provided insufficient fish for year-round fishing. The Federal Department of Fisheries imposed the quota split in favor of the inshore boats which have proliferated and caused an over-capitalization during the last five years. Over-capitalization will be a major cause of a decrease in profitability of fishing and processing operations in the 80's.

Requirement for Year-Round Processing

The industry is increasingly becoming a seasonal operation because of various regulations and efforts by the Federal and certain Provincial governments. This move must be reversed to permit efficient year-round operation of plants and to maintain fully employed personnel. Modern plants require vessels which fish year round and thus demand a viable offshore fleet. In a Federal government study in Newfoundland (Nicholson, in lit), the seasonal plants were estimated to be used at 45%, while offshore plants were utilized to at least 65% of capacity. Simple economic projections on processing and fishing costs clearly show the incorrect management approach in this issue that has been taken by Federal management officials. The increase in seasonality of fishing has been seen by the proliferation of new vessel licenses during the last decade, during a time when the number of vessels operating offshore has actually decreased. In southwestern Nova Scotia alone, an estimated 750 new inshore licenses have been allowed, and in the Atlantic region as a whole, the number probably approaches 2500. Quota allocations have removed the offshore fleet from the Gulf of St. Lawrence area, and have restricted fishing on the Scotian Shelf. Large trawlers are now barred from 50% of the groundfishing grounds, but 3 years ago they were barred from only 30%. There is no doubt that in certain areas it is best to remove large wetfish trawlers, but a balance is required in the industry which is not being maintained.

Control of Technology

Government managers have tried to control fishing activities and efficiencies by controlling new technologies: for example, the 125% vessel replacement rule, which allows owners to replace their boats by a maximum increase in length of 25% over their existing vessel, and control of freezer vessels to a limit of 200 feet. When one starts to control technology, inefficiencies are bound to appear. Thus more effective methods of control of the resource itself are needed rather than attempts to regulate the industry by impeding the development of implements required for efficient harvest. In farming, Agriculture Canada does not try to control the size of the harvest by controlling the horsepower of tractors.

Collective versus Individual Standards in the Fishing Industry

Hitherto, the market has dictated the exploitation of fish stocks and this has led to the disappearance of the resource and emasculation of the industry. The result has been agreement by the industry of measures to understand the biology of the resource and to control its harvest. There remain a number of attitudes rooted in this history that require modification in the 80's. Some of these are discussed. It is clear that the quality of the product plays a role in the share of the international market enjoyed by the Canadian fishery. Yet a fish buyer on the wharf is always under pressure to keep his plant supplied with fish. If only second class fish is available, he buys it because he knows that a second buyer stands ready to take the catch, a second buyer who will inevitably have preference the following day. Thus the decision of the buyer to take inferior fish is correct from his point of view but incorrect as the collective industry in the context of developing a product of highest quality.

Similar considerations apply to inaccurate reports of the size of the catch by fishermen who consider such practice to be a personal gain in the total fishery (CAFSAC 1980). As such information is the basic data whereby fish stocks are managed, this behavior inevitably leads to managed fishing.

Fishing is still considered a part-time employment, and the Government has aided and abetted this way of life by requiring 12 weeks employment in the fishery to qualify for year-round unemployment insurance benefits. In fact, fishing has been subsidized by transfer payments to U.I.C. from so-called better-off provinces such as Ontario, Alberta and British Columbia. These unethical U.I.C. rules have often forced a part-time fishery.

The Role of Government in the Fishing Industry of the 1980's

There are 3 facets of the Government's role in the fishing industry that need clarification as soon as possible.

The first concerns which level of government has jurisdiction over the regulations governing control of the resource. Looking specifically at the Atlantic coast, there are 5 separate provinces struggling to gain an authoritative input into the fisheries policies that will apply to each of their supposed jurisdictions. However, common sense will tell anybody who takes time to study the situation that the fishery is a Canadian resource that is not divisible by provincial boundaries. Most of this confusion has arisen by Federal dictates on policy which have ignored local wishes and have often been decorated by advisory committees sitting after the policies had been decided. I believe that the Federal jurisdiction must be maintained but a management and policy setting group should be locally situated. Such a council or group should have a competent staff of representatives from each of the 5 Atlantic provinces, the Federal Government, and both sides of the industry. This council would then set practical fisheries policy and implement it.

Secondly, better relations between Government and the industry are required. In general, regulations need to be simple and clearly enunciated; the least possible government involvement is the most desirable. Thus an explicit, long-term national fisheries policy based on the principle of resource protection is required to permit fishermen and processors to know where they stand and how they should plan their future.

Thirdly, there is a need for greater efficiency in the relationship between government and the industry. This involves education by the government to enable fishermen to become more market-oriented, to be acquainted with new techniques, involving not only equipment but improving knowledge of the scientific basis of the resource. Contrariwise, there is a need for a more streamlined management structure in the Federal Civil Service. More than 5,000 people are employed by Fisheries and Oceans, and the size of the Canadian fishing industry is about 2.5×10^4 man years in the primary resource sectors. In Iceland, where the fishery lands about twice the tonnage of fish landed in Canada and where quality is extremely high, about 250 civil servants are responsible for management. It is clear that the Canadian management structure is inappropriate for the industry. There seems to be a case for financing the management of the industry by imposing a levy on each pound of fish landed. This would encourage economy, as the industry could not afford exhorbitant levies, nor poor resource conservation.

Research in the 80's

In the 1980's, research, both applied and academic, is required in various areas. These encompass areas of engineering, biology, economics, and biochemistry.

Quality retention research to improve the quality of the product now marketed is a necessity and must include work from the catch to the market.

Comprehensive industrial engineering and operations research is required at the vessel and plant level to develop and implement new and more efficient fish handling and processing methods. Imaginative engineering design of fish processing equipment to reduce cost and increase yields will be required in the 80's.

Greater utilization of the fish that is landed must be obtained in the 1980's. This will require research into use of offal for greater food and pharmaceutical usage. Presently, two-thirds of the fish goes in the offal chute and, at best, is dried for meal.

Pressure on reducing the cost, in terms of dollars and fuel usage of fishing, will necessitate continued research into better understanding of fish behavior, fish finding, remote sensing of fish, and operations research into fishing.

Better understanding of exploited multi-species biology and management regulation will be needed as management of the total economic resource is required to optimize the potentials available in our fishing areas.

Continued resource and technology development on under-utilized species is required to develop knowledge of the species, and to develop harvest and utilization methods and markets.

Aquaculture research on selected resource-limited species such as lobsters is necessary. Approximately 6 to 8% of the weight of fish landings in the world is cultivated by man. The majority of these are from Asian and Pacific-rim countries. Canada lags most parts of the world because our resources have tended, in the past, to be market limited. For species such as lobsters, we have become resource limited and aquaculture research is called for to develop additional procurement sources.

Industrial pollution has been the demise of a number of the fresh-water lake and river fisheries in Canada. Investigative research in the level of damage already inflicted on the marine fisheries is required. Already some fisheries have detectable levels of PCB and pesticides in the fish. Fear also has been expressed that the sexual fecundity of some stocks may be endangered by pollution. Research, funded by government, is required to investigate the levels and potential harm of continued production.

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THE IMPACT OF FUNDAMENTAL RESEARCH ON THE FOREST INDUSTRY IN THE MARITIME PROVINCES

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Selected research topics in several scientific disciplines are reviewed in the context of their potential or demonstrated value to the forest industry in the Maritime Provinces.

Introduction

I should like in the course of this paper to discuss several studies which might be described as fundamental or basic research, and which have had or potentially could have directly or indirectly an important impact on forest-based industry in this region. My selection of topics is personal and subjective. It reflects my association with the Canadian Forestry Service (indeed much of the research which I shall discuss has been carried out by C.F.S. scientists); it also bears the stamp of my own research interests as an organic chemist. I only hope that it does not reflect too strongly my ignorance of the forest itself!

Having flaunted the term "fundamental research" in my title, I feel obliged to add something of a disclaimer! The distinction between fundamental research and applied research is not, I think, an important one. It is clear that much research relating to forestry, or other disciplines for that matter, does not fit neatly into classifications such as "fundamental" or "applied". One can of course recognize differences in objectives and motivation that give rise to these labels. If, however, we accept that *all* true research is concerned with generation of new knowledge, and surely is motivated at least in part by curiosity, then the "applied/fundamental" dichotomy loses much of its significance.

The distinction, nevertheless, is made and used by research administrators, funding agencies, and many scientists, and in recent years it often seems that the scales have been tipped in favor of "applied" (presumably equated with "useful") research, undoubtedly as a result of political expediency. History ought to teach us that both basic and applied research are essential to our development, and that neither alone can prosper for long. Nobel Laureate, Dorothy Hodgkin, in her presidential address to the British Association for the Advancement of Science in 1978, recognized the difficulty in deciding how to classify research. I quote from an account of her talk (L.K.H. 1978): "She described a recent study by Comroe and Dripps which evaluated the scientific papers that have contributed to advances in clincial medicine. Of 529 papers, 41% were not clinically oriented at all and 62% could be described as basic research. They concluded that, in general, basic research paid off twice as handsomely as all other kinds of research and development combined. Hodgkin cited insulin as a case in point. 'If we knew in all fundamental detail how insulin acts to control our metabolism we might be able to devise far better methods for treating the different disorders associated with diabetes.' "

I would like to paraphrase Professor Hodgkin's reference to insulin in a forestry context and suggest that if we knew in all fundamental detail how the forest ecosystem works, we would be able to devise far better methods for managing our forests.

Forestry in the Atlantic Region

Let us try to put the importance of the forest resource in perspective by examining some figures (Fraser 1979).

Thirty-five percent of Canada's land area is covered by forest, of which over two-thirds can be classified as productive and accessible forest land by today's standards.

The forest resource provides jobs either directly or indirectly for over 10% of the nation's labor force. Exports of forest products currently total $9 billion and account for 18% of our exports: they make a greater net contribution to Canada's trade balance than agriculture, fishing, mining, and fuels combined.

Much of the importance of the forest, of course, lies in less tangible contributions, such as regulation of water flow, sheltering of wildlife, etc. but these are beyond the scope of the present discussion.

The economy of the Maritime Provinces is linked especially closely with the forest resource, as clearly illustrated in statistics compiled by Runyon (1979).

> "Forest land area in the Maritime Provinces is about 110,000 km^2 or 85% of the total land area compared to 37% for all of Canada.
>
> Privately owned forest land in the Region is about 62% of total forest land, compared to 6% for Canada.
>
> There are 845 million m^3 of merchantable wood in the Maritimes or enough to build over 30 million houses. Softwood species make up 81% of this volume.
>
> Estimated direct revenue from nonconsumptive uses of forest and forest land (fishing, hunting, trapping, etc.) is over $5 million.
>
> Average primary forest production (1972-1976) is more than 11 million m^3 most of which is pulpwood. This represents a pile of wood 1m high and 1m wide stretching from Fredericton to Vancouver and back.
>
> There are some 662 logging and manufacturing establishments in the Region which purchase $675 million worth of fuel, electricity, materials and supplies.
>
> Direct employment in forest industries is over 21,000 with an estimated 40,000 jobs generated indirectly. Salaries and wages amount to more than $250 million.
>
> In New Brunswick, one of every five persons employed in goods-producing industries works in forestry or related manufacturing. Pulp and paper mills rank first and sawmills second in terms of wages paid within the manufacturing sector.
>
> In Nova Scotia, one of every 13 persons employed in goods-producing industries works in forestry or related manufacturing. Pulp and paper mills rank second and sawmills fourth in terms of wages paid.
>
> Value added from forestry and related manufacturing in the Region is over $500 million.
>
> In New Brunswick, value added from logging operations alone is higher than for agriculture, fishing, or mining.

> Forestry and related industries account for about 10% of gross domestic product in New Brunswick, 4% in Nova Scotia and less than 1% in Prince Edward Island.
>
> Value of shipments of forest products for this Region in 1976 was over $1.1 billion.
>
> Value of exports from New Brunswick and Nova Scotia outside Canada is over $650 million or 50% of all exports.
>
> In New Brunswick, forest product exports comprise over 60% of all exports compared to 5% for agriculture, 7% for fish products, and 14% for mining and mineral products.
>
> In Nova Scotia, exports of forest products in 1976 were 31% of the value of all exports, while agriculture goods were 5% and fishing, 27%."

The Spruce Budworm

As the forest industry, particularly the fiber industry, has developed in eastern Canada, balsam fir, once considered a weed species, has become of central importance to the economy. This development has had the effect of putting us into direct competition with the spruce budworm, formerly, in its own way the undisputed chief harvester of fir, but not considered a major economic pest. As a result, during the last 3 or 4 decades, the spruce budworm, *Choristoneura fumiferana*, has received the lion's share of attention from the forest research community in this region.

It has become increasingly clear that forest management strategies to maximize our portion of the resource can only be devised on the basis of an in-depth understanding of the budworm, its population dynamics, and the forest ecosystem of which it is a part: this is fundamental research with very practical implications!

At endemic population levels, the insect constitutes no more of a problem than any of a dozen other defoliator species which share the same host trees. With a mere handful of larvae if any per tree, the impact of budworm feeding activity on the foliage is barely perceptible. The notoriety of the spruce budworm stems from its periodic outbreaks in fir-spruce stands over immense areas, when populations in the course of 5 or 6 years may jump from half-a-dozen larvae per tree to an estimated 20,000! Few trees can sustain feeding at this high level for long, and widespread mortality of balsam fir usually results within a few years of the peak of such an outbreak (Miller 1975).

Extensive studies conducted at Green River, New Brunswick between 1945 and 1970 have provided the basis for much of our present knowledge concerning the dynamics of spruce budworm populations (Morris 1963).

It is useful to look at the pattern of the insect's life cycle (Fig 1) as a prelude to considering its interaction with the forest ecosystem and its population dynamics.

Several features of the cycle are noteworthy in the context of budworm population dynamics: The number of eggs laid per female, for instance, indicates that only about a 1% generation survival rate is required to maintain a constant population. Dispersal is a major cause of mortality of small larvae, and adult dispersal can bring about massive shifts of populations. The survival of large larvae has been identified as one of the most significant factors determining population trends. The stage at which major feeding occurs, and, in general, synchronization of the cycle with host-tree phenology have an important bearing on the interaction. A major factor determining the occurrence and severity of outbreaks is the distribution, age, and condition of balsam fir, the most favorable host for the budworm (Fig 2).

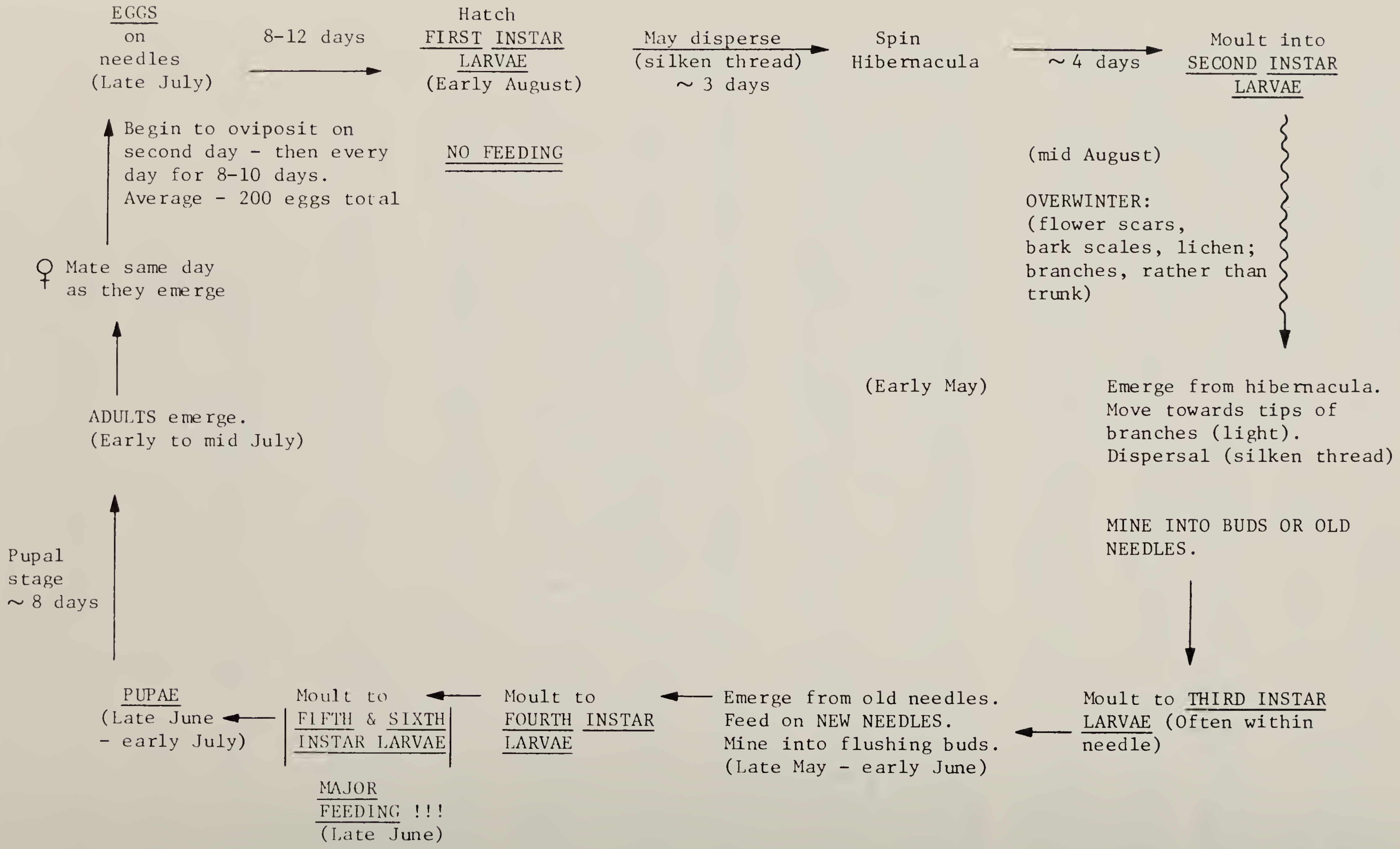
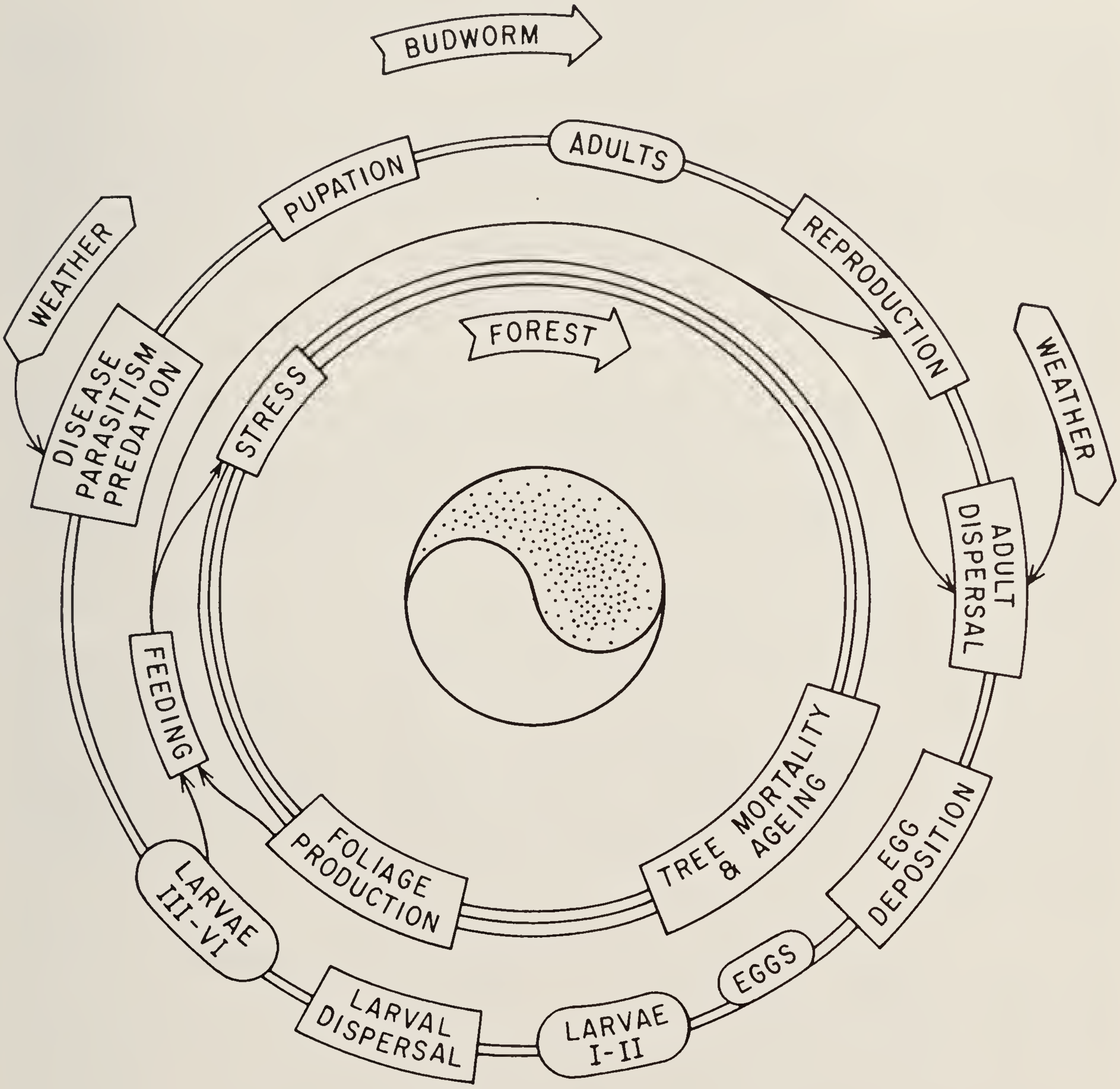

EGGS on needles (Late July)
8-12 days
Hatch FIRST INSTAR LARVAE (Early August)
NO FEEDING
May disperse (silken thread) ~ 3 days
Spin Hibernacula
~ 4 days
Moult into SECOND INSTAR LARVAE
(mid August)
OVERWINTER: (flower scars, bark scales, lichen; branches, rather than trunk)
(Early May)
Emerge from hibernacula. Move towards tips of branches (light). Dispersal (silken thread)
MINE INTO BUDS OR OLD NEEDLES.
Moult to THIRD INSTAR LARVAE (Often within needle)
Emerge from old needles. Feed on NEW NEEDLES. Mine into flushing buds. (Late May - early June)
Moult to FOURTH INSTAR LARVAE
Moult to FIFTH & SIXTH INSTAR LARVAE
MAJOR FEEDING !!! (Late June)
PUPAE (Late June - early July)
Pupal stage ~ 8 days
ADULTS emerge. (Early to mid July)
♀ Mate same day as they emerge
Begin to oviposit on second day - then every day for 8-10 days. Average - 200 eggs total

Fig 1 Life history of the spruce budworm.



PROCESS CYCLE
OF THE BUDWORM FOREST SYSTEM

Fig 2 The process cycle for the budworm forest system. The inner ring represents the forest cycle, the outer ring the budworm cycle. Ellipses indicate insect life stages; arrows show causal relationships among processes and insect life stage densities. After Jones (1977).
Reproduced from W.C. Clark (1979) PhD thesis. University of British Columbia.

The overall picture which emerges, when we take into account the effects of biocontrol agents, weather, the composition and condition of the forest, etc. is a highly complex one with so many variables that it becomes virtually intractable. For this reason, mathematical models are currently finding favor as a method for organizing information on the dynamic behavior of the budworm-forest system (Baskerville 1976). Simulation models may prove to have great value in predicting in advance the consequences of various possible management strategies.

New Approaches to Forest Protection

While improved forest management and silvicultural practices may help to reduce our dependence on conventional chemical pesticides, it seems certain that some kind of insect control agents will remain a component of future integrated management approaches. Yielding to my chemical proclivities, I shall not elaborate in greater detail on the highly important areas of population dynamics, forest management and silviculture, but shall single out 3 recent "chemical-biological" approaches to insect control which might potentially supplement, if not supplant, the broad spectrum insecticides currently used against the budworm. I shall refer to the sex pheromone, insect growth regulators, and anti-feedants.

The Sex Pheromone

Let us consider first the sex pheromone of the spruce budworm, which has been identified (Weatherston et al. 1971; Sanders & Weatherston 1976) as a mixture of the E and Z isomers of 11-tetradecenal (Fig 3), in the approximate ratio 96:4. Several chemical synthetic routes have been developed, and the material is available in quantity for biological studies, including testing for mating disruption of the budworm in the field.

What is the function of the pheromone from the insect's point of view, and how can it be exploited for controlling budworm populations?

Investigations by Seabrook and collaborators at the University of New Brunswick, and by Sanders at the Great Lakes Forest Research Centre, indicate that in addition to its role as a long-range attractant, enabling male moths to locate their mates over a distance, the pheromone is also involved in initiating mating behavior patterns in the male. Thus, moths already in close proximity (for instance in high density populations) are most likely to mate during the evening while the female is releasing her pheromone.

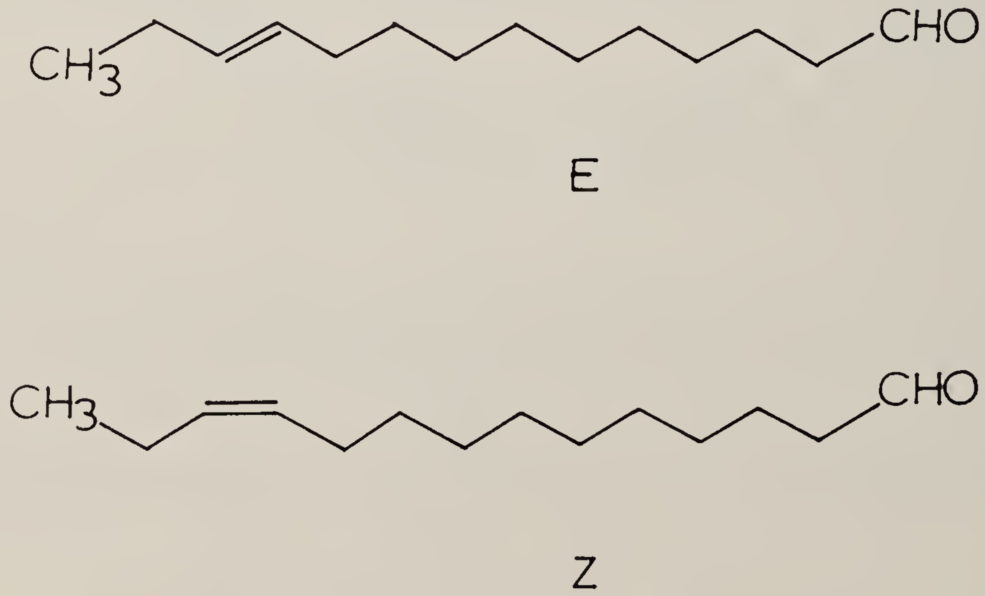


Fig 3 E and Z isomers of 11-tetradecenal

It is possible that the budworm's chemical communication system may be more complex than it appears on the basis of our present knowledge. Studies by P. Silk and C. Wiesner at the New Brunswick Research and Productivity Council could help to shed further light on the pheromonal interaction. These researchers are examining trace components in the effluvia and abdominal tips of virgin female moths, using inter alia, the powerful technique of combined gas chromatography—mass spectrometry. They and Seabrook's group are also seeking to determine whether or not a male pheromone is involved in the communication system.

The question which concerns the forest manager is: what is the potential of the sex pheromone for controlling budworm populations? At low to medium population densities where the male moth clearly depends on the pheromone to locate his mate, there are precedents to suggest that distribution of a large number of point sources of pheromone throughout the insects' range will confuse the males, and cause a reduction in male-female encounters. Suppression of budworm mating is indeed observed under such conditions in small-scale experiments with the pheromone.

Even more interesting, however, from the operational point of view, is the observation by the University of New Brunswick research group that when high density populations of budworm moths in cages (simulating outbreak conditions) are exposed to appropriate levels of pheromone, substantial reduction in mating also occurs. In such high population densities it seems unlikely that the male moth would experience difficulty in locating a mate, even without the guidance of pheromone, so mechanisms other than simple confusion must be responsible for the mating suppression. One such mechanism may be indicated by Seabrook's finding that exposure to concentrations of pheromone higher than the natural levels causes adaptation or blocking of the male's sensory system. There is also evidence which suggests that the female's own response to such levels of pheromone might contribute to a reduction in mating.

The true potential of the pheromone for controlling budworm populations can only be evaluated on the basis of a series of carefully conducted field trials, designed so that the effects of immigrating gravid female moths can be eliminated. Research along these lines is in progress.

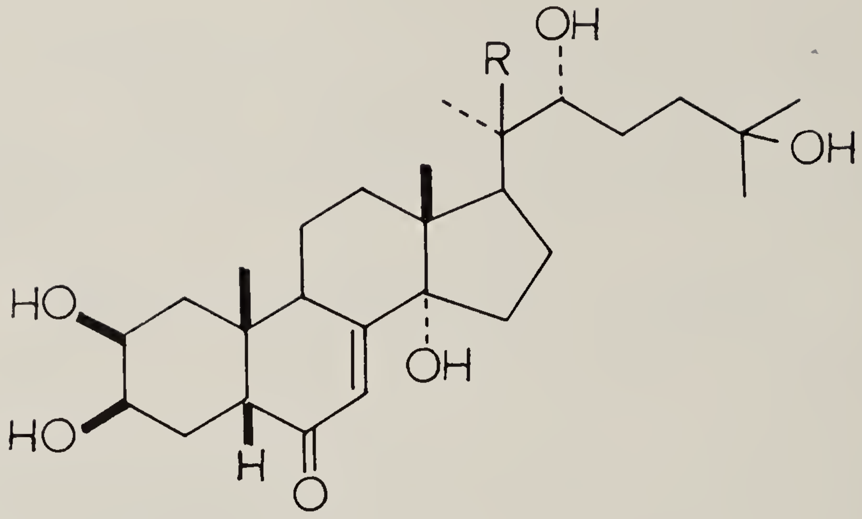
The problem of developing a suitable formulation which will ensure continuous release of the pheromone at appropriate levels for the required period (ca 3 wk) remains a formidable one, and calls for further extensive experimentation.

Another dimension has been added to the pheromone studies by University of New Brunswick chemists Z. Valenta, J.A. Findlay, and G. Lonergan who have prepared synthetic analogues of the natural material. Some of these compounds have displayed interesting biological properties in preliminary tests, and one shows a significant synergistic effect when used in traps with the natural pheromone.

From the foregoing discussion one may conclude that it is still too early to predict the extent to which pheromone-induced suppression of budworm reproduction will find use as a forest management tool.

My personal guess is that while pheromone will not be a panacea (there are no panaceas in forest management!), it could well play a significant role as a component of future integrated pest management programs.

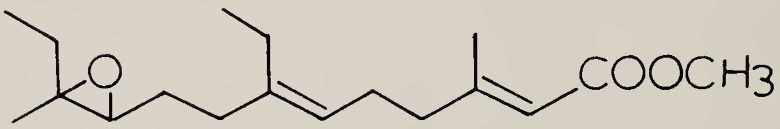
My discussion of the other "chemical-biological" approaches to which I alluded earlier, will be brief, and will be confined to description of the principles involved, as in contrast with the pheromone work, these have not yet progressed beyond the conceptual stage. I mention them mainly because of our own interest and involvement in this research.



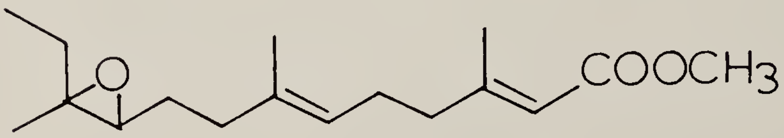
α - Ecdysone R = H

β - Ecdysone R = OH

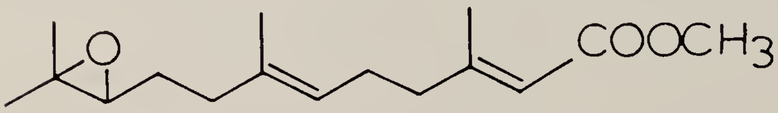
Fig 4 Alpha and beta ecdysone



JH I



JH II



JH III

Fig 5 Juvenile hormones

Insect Growth Regulators .

While the development and metamorphosis of insects has fascinated philosophers and naturalists from time immemorial, by far the most dramatic progress towards our understanding of these phenomena has resulted from the research of contemporary insect physiologists such as V.B. Wigglesworth and C.M. Williams, not forgetting the important contributions of their biochemical and chemical colleagues. Their research has demonstrated that moulting and metamorphosis are under endocrine control, and that 3 major classes of hormones are involved (Rees 1977).

The brain hormone, characterized as a peptide, is produced by neurosecretory cells in response to various stimuli. The action of brain hormone on the prothoracic gland triggers the synthesis and release of the moulting hormone, ecdysone (Fig 4).

A third hormone (Fig 5), the juvenile hormone (JH) is produced by a gland known as the corpus allatum, which is under direct neural control from the brain.

Ecdysone induces the events associated with each moult. JH determines the morphological outcome of the moult by suppressing adult differentiation in favor of larval structures.

"High" levels of JH therefore favor a larval-larval moult, while a drop in JH titre results in a larval-pupal moult. JH is virtually absent at the pupal-adult moult (Rees 1977). Juvenile hormone or JH analogues applied exogenously at these last stages disrupt the normal development pattern of the insect, and thus have potential as insecticides. Indeed, JH mimics constitute one of the interesting groups of insecticides known collectively as insect growth regulators, some of which have already been used operationally.

Such insecticides, however, hold little promise for controlling insects like the budworm, which inflict their major damage at larval stages before they are vulnerable to exogenous JH.

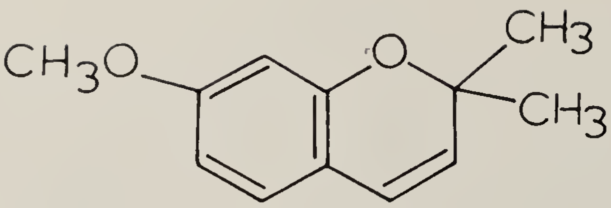
An alternative approach is suggested by the observation of Williams (1961) that surgical removal of the JH-producing corpora allata of the *Cecropia* silkworm during the last larval instar, led to pupae which possessed, prematurely, a number of adult characteristics.

Bowers et al. (1976) subsequently isolated 2 simple chromene derivatives, the precocenes (Fig 6), from the common bedding plant *Ageratum houstonianum*, which had the remarkable property of apparently disrupting JH production by the corpora allata of several hemipteran insect species.

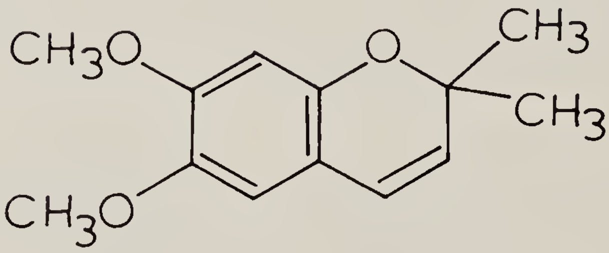
Precocenes, added at an early instar stage resulted in precocious moulting to unviable adults! Unfortunately the precocenes, simple natural products readily amenable to chemical synthesis, do not display this activity against the lepidoptera tested so far, including the budworm.

An approach differing from the extensive screening which showed up the precocenes is being pursued in our laboratory. We focus our attention on the JH I molecule. The biochemical pathway through which JH I is built up is understood in some detail, largely as a result of independent studies at the Zoecon Corporation and Texas A and M University (Rees 1977). The pathway appears to be unique to insects. The objective which we have set ourselves is to discover a compound which will specifically inhibit an enzyme catalyzing one of the biosynthetic steps to JH I. The consequent suppression of the JH level might then be expected to lead to precocious metamorphosis, as produced in hemiptera by the precocenes.

Several candidate compounds have been synthesized in our laboratory, and although none to date has shown the desired effect, this study is continuing, not without optimism.

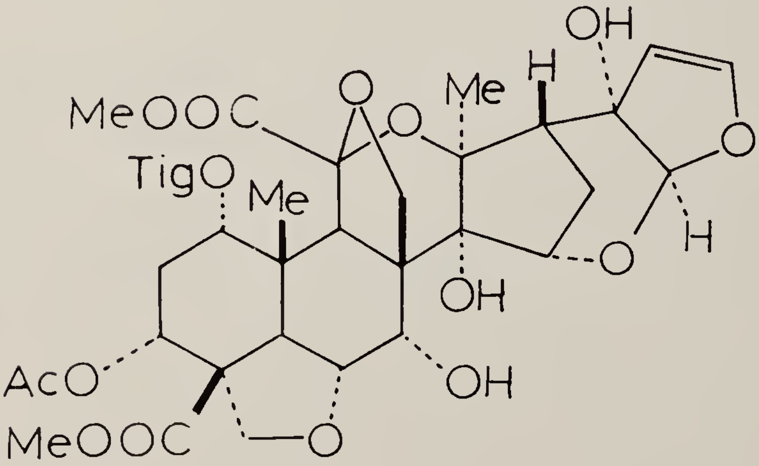


Precocene 1



Precocene 2

Fig 6. Precocenes from *Ageratum houstonianum*



Azadirachtin

Fig 7 Azadirachtin

Antifeedants

The third of the "chemical-biological" approaches to budworm management which I want to mention is the possible exploitation of natural antifeedants.

For many insects, the selection of a particular host plant for feeding is influenced, at least in part, by the presence in the foliage of phago-stimulants or -deterrents. Included among the latter are antifeedants, defined by Kubo and Nakanishi of Columbia University as substances which when tasted can result in cessation of feeding, either temporarily or permanently depending on potency (Kubo & Nakanishi 1977).

One of the most powerful insect antifeedants known is azadirachtin (Fig 7), isolated from leaves and berries of *Azadirachta indica*, the Indian neem tree. This compound, investigated by E.D. Morgan and co-workers in England, and by K. Nakanishi and his group in the United States, exhibits strong antifeedant activity against a number of insect species, but most notably *Schistocerca gregaria*, the desert locust. These insects will starve to death rather than feed on leaves which have been surface-treated with only a few nanograms of azadirachtdin per square centimeter! The compound does not appear to be generally toxic: neem sticks are chewed in parts of Africa and India to clean the teeth, and are also used as a remedy against malaria. Furthermore, berries of the tree constitute the favorite diet of several bird species (Kubo & Nakanishi 1977).

Recent entomological and chemical literature contains a growing number of reports of compounds (usually though not necessarily of plant origin) possessing anti-feedant activity against various insects. The activity may be detected by direct or indirect observation of feeding inhibition or by electrophysiological methods.

Antifeedants display a wide diversity of molecular structures, and many appear to be specific to certain insects. Little is known so far concerning the details of their mode of action. The possibility of finding antifeedants specific to certain insects and devoid of toxic effects on other organisms presents an exciting prospect in the context of pest control. For instance, reduction of feeding by budworm larvae through the agency of such a compound would not only have the effect of saving foliage, but the resulting physiological stress would reduce the vigor of the population and enhance the effects of natural mortality factors.

A mutual interest in discovering antifeedants for the spruce budworm has evolved into a collaborative research program between our laboratory and scientists at the University of Maine. At Orono, entomologist D.E. Leonard and chemist M.D. Bentley have developed a convenient and reproducible assay for observing antifeedant effects on sixth instar budworm larvae. Given an adequate supply of larvae, the method is suitable for an extensive screening program of non-host plant extracts and other materials. The Maine scientists have already tested more than 100 extracts and have observed some encouraging results. Additional extracts are being prepared in our laboratory.

Extracts which show promising antifeedant activity in the initial screens are fractionated into their constituents using standard chemical separation techniques. The fractions are monitored by bioassay, and material possessing the desired activity is purified. The molecular structure of the pure antifeedant may then be elucidated through chemical and physical studies.

A compound which displays strong antifeedant activity against the budworm in the preliminary tests must satisfy additional criteria before it can be considered as a potential control agent: its toxicity must be low, and it needs to be readily and cheaply available in quantity, either by extraction from natural sources or by synthesis.

The discovery of such an agent would add an invaluable new dimension to current strategies aimed at reducing damage caused by the spruce budworm.

Biological Control and the Winter Moth

In my brief reference to the population dynamics of the budworm I mentioned the influence of biocontrol factors, namely the predators, parasites, and disease organisms which have co-evolved with the insect in the forest ecosystem. How effective are these factors in regulating populations, and how does population density influence their effectiveness? What happens when extraneous factors are introduced which disturb the natural complex?

The answers to such questions have important implications in the planning of forest management strategies.

In the budworm-forest system (free from the intervention of *Homo sapiens*) insect populations have periodically risen to outbreak proportions, notwithstanding the existence of many natural enemies. The evidence indicates that there have been 6 or 7 such major outbreaks in eastern Canada during the past 200 years, each extending over millions of acres. As an outbreak situation develops, the budworm population at some stage exceeds the capacity of predators and parasites to contain it, and it then rises explosively until other factors eventually cause the population to collapse.

Baskerville (1975) argues that periodic outbreaks of the budworm do not indicate ecological instability of the budworm-forest system as a whole, when measured on a time-scale appropriate to the system function (50-100 yr). Indeed, he has termed the insect "super silviculturist", as its activities result in the development of successive generations of forest favorable to future generations of budworm: together they constitute a self-regulating system.

In contrast with the budworm, many native insects which could potentially be pests are in fact maintained at moderate levels by the action of parasites, predators, and disease. On the other hand, introduced species may become serious problems just because the biological agents which control their populations in their native habitat have been left behind (Balch 1960).

Whereas attempts to promote either indigenous or exotic biological control agents for regulating populations of native insect pests, such as the budworm, have not been fruitful so far, the approach holds great promise in combatting introduced insects which have become pests for the reasons just cited.

I would like to discuss one example of the successful application of biological control of such an introduced insect pest, which has particular relevance to this Province. Cast in the role of villain in this story was the winter moth (*Operophtera brumata* L.), apparently introduced accidentally from Europe into the eastern seaboard of North America via Nova Scotia (Embree 1971).

The winter moth is a serious defoliator of hardwoods and during the decade following its introduction, it wreaked havoc, particularly in Nova Scotia oak forests, with associated economic losses at today's values reaching millions of dollars. Had the insects' depredations continued, most of the oak now standing in Nova Scotia, estimated to be more than 1.5 million cords, would probably have been lost.

Credit for checking the infestation is shared by two parasites of the winter moth, deliberately introduced from a generally endemic environment in Europe. Following initial experiments and observations by A.R. Graham, D.G. Embree, a native of the Province working with the Canadian Forestry Service, led the control project and conducted the associated research on population dynamics of the host and parasites.

More than 60 parasites of the winter moth are known and presumably contribute to the regulation of its populations in Europe. Six species were selected and introduced in Nova Scotia during the period 1955 to 1960. Four of these were not

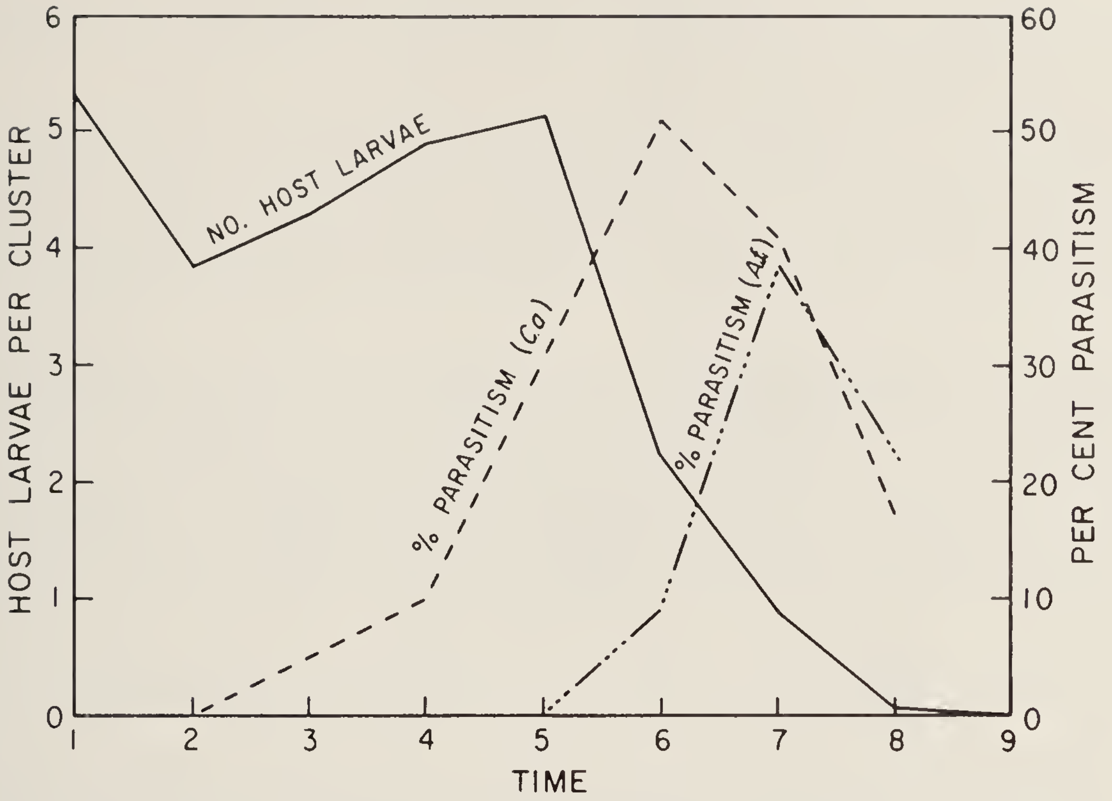


Fig 8 Typical history of a winter moth infestation and parasitism by *Cyzenis albicans* (Fall.) and *Agrypon flaveolatum* Grav.). Time refers to the number of years the outbreak persisted (Embree, 1966).

subsequently recovered, but 2, *Cyzenis albicans* (Fall.), a tachinid fly, and *Agrypon flaveolatum* (Grav.), an ichneumonid wasp became established, resulting within a few years in the collapse of the winter moth outbreak (Fig 8).

Embree (1971) points out that in 1954 when the study began, hardwoods were not extensively utilized in Nova Scotia, so that the winter moth was not deemed a major economic pest. Today on the other hand, paper and hardboard-producing mills designed to use hardwoods make an important contribution to the Province's economy. He adds wryly that if these mills had existed in the 1950's, it is likely that attempts to control the winter moth would have been based on the use of insecticides, because the success of the biological control program could not have been predicted.

The Nova Scotian experience has provided the stimulus for applying the same method in British Columbia, where an isolated population of the winter moth has appeared in the last 3 years. Parasites have been collected from surviving populations of winter moth in Nova Scotia and are now being released in Victoria, where the winter moth is feeding on Garry oak throughout the city.

Tree Improvement

Having devoted much of the foregoing discussion to insects which damage trees, I should like now to mention briefly some research which relates more directly to the trees themselves. Specifically, let us consider some aspects of the domestication of forest trees, an activity whose importance is being increasingly recognized in eastern Canada, as gloomy forecasts of wood shortages before the end of the century emphasize the finite nature of the forest resource.

Currently some 60 million trees, mainly spruces and jack-pine, are planted annually in the Atlantic region. This number is expected to rise to 100 million trees annually by 1985. By the time currently planted seedlings are 40 years old, it is projected that 20% of the region's forests will be of man-made origin (Fowler 1980 *in verb.*) Attempts to optimize productivity of this cultivated forest are based on application of the art and science of tree breeding, nourished by research in genetics, tree physiology, ecology, and wood science.

The ultimate use of the crop will determine what characteristics are desirable in the cultivated tree: for example straight trees are obviously preferable for lumber production, but straightness is of little consequence to the paper industry, where fiber length is more important. Optimum growth performance, which is reflected in wood yield, is the single most important characteristic sought, regardless of the end use.

At first sight the domestication of trees might be expected to follow a pattern similar to that for other crops. Considering that for corn, genetics and intensive farming practices have increased yields perhaps 16-fold relative to the primitive wild corn plant (Rediske 1974), the implications for forestry are interesting indeed! However, problems of scale and long generation times present formidable difficulties to the tree breeder, not encountered by his counterparts in agriculture or horticulture.

How then does one go about large-scale production of genetically improved trees?

While hybridization experiments, usually intraspecific, sometimes yield interesting results, the most promising approach to tree improvement at present is the process of selection and breeding, based on the natural genetic variability of certain characteristics.

So-called plus-trees are first selected from the wild population. As part of this process the tree breeder attempts to sort out the relative contributions of genetics and environment in producing the desirable phenotype.

The trees of interest are those that in a given environment will be most productive, according to the criteria which have been set.

The usual method of mass producing genetically improved trees is by establishment of seed orchards on carefully chosen sites. In seedling seed orchards, progenies from the selected plus-trees are planted in an orchard pattern which is designed to maximize interpollination of the desired phenotypes. Alternatively, for many species, clonal seed orchards, based on grafts from the selected trees, have been found to be more effective in terms of genetic gain. In both kinds of orchards, culling procedures ensure that only the better genotypes are retained for final seed production.

The genetic gain which can be realized by propagation of selected plus trees is illustrated graphically in Figure 9 (courtesy of J.M. Bonga).

Plotting growth rate against frequency of occurrence of that rate, we obtain a normal distribution curve as shown (Rediske 1974). Plus trees are selected from the high growth end of the curve. The genetic gain from sexual reproduction of the plus trees is manifested as a displacement of the maximum, while decreased variability may lead to a narrowing of the base of the curve. Genetic gains of 10-20% are possible in the progeny, and these gains may be further enhanced in subsequent breeding phases (Rediske 1974).

While vegetative propagation in principle makes possible the retention of all the genetic components of the parental genotype, the method at present does not lend itself to mass production of most coniferous trees. The problem is that as a tree matures, it becomes increasingly difficult to propagate vegetatively, other than by the time-consuming process of grafting.

The use of tissue culture techniques might provide the key to vegetative propagation on a mass scale. However, although many plants have been successfully propagated by tissue culture, tissue from mature conifers has thus far proved obdurate. Callus from trees sufficiently mature to be recognizable as genetically superior has

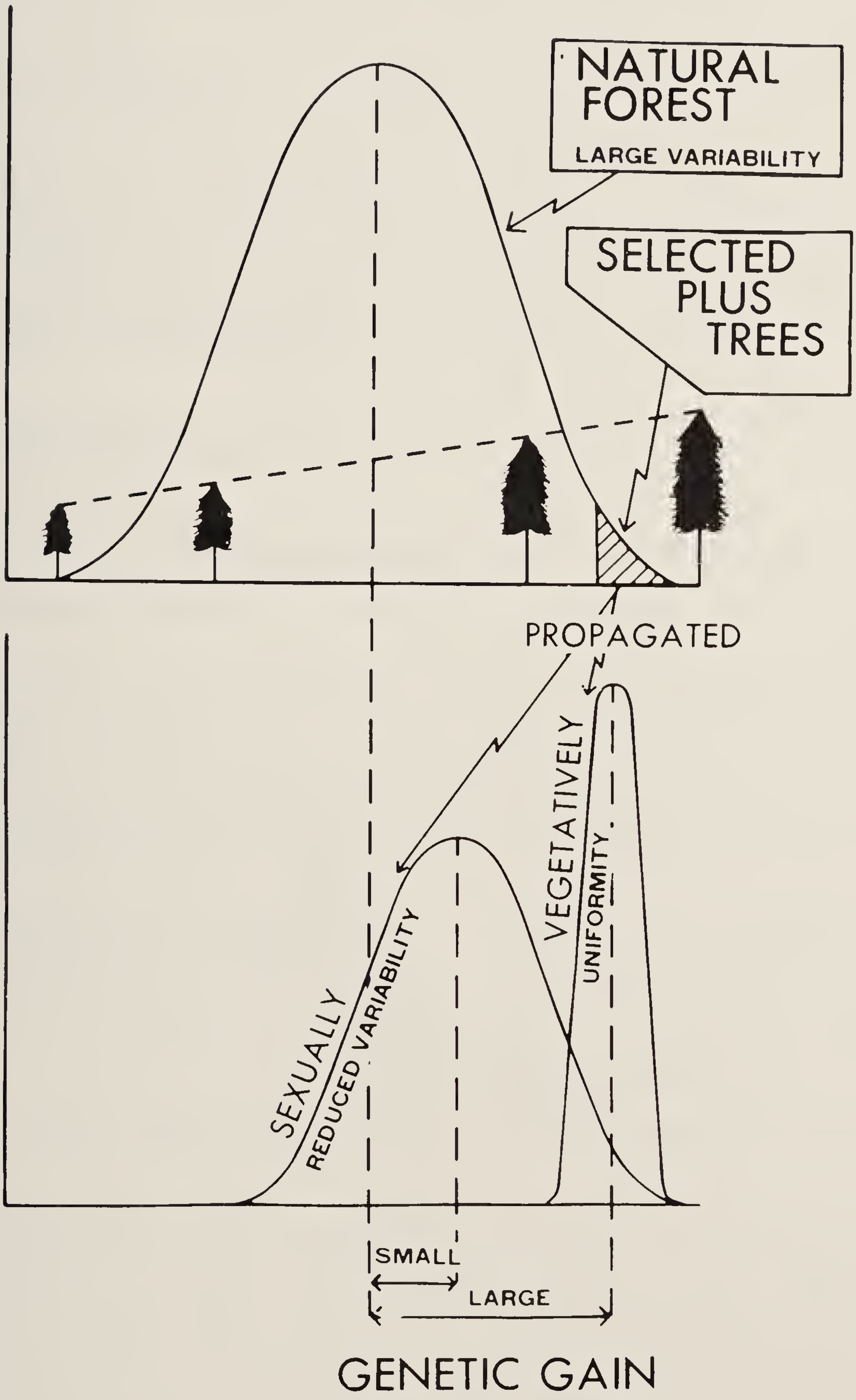


Fig 9 Genetic gain through propagation of selected plus trees.

yet to be induced to form differentiated structures. The search for a solution to this problem, which could make tissue culture an invaluable tool in tree improvement, remains a challenging research objective.

I alluded earlier to the problems posed to the tree breeder by the long generation time of his crop. Identification and evaluation of the best performers among parental or progeny generations may take 15 years or more. In attempts to develop methods to accelerate progeny ranking, several lines of research have been pursued. One interesting approach is based on studying correlations between photosynthesis and growth rate, in the hope that net photosynthesis, as measured by carbon dioxide uptake, could be used for early identification of growth potential.

Another time-related problem concerns flower initiation. As the juvenile tree is vegetative rather than reproductive in its growth pattern, the production of male and female strobili does not occur for several years. Research indicates that these patterns are regulated by hormones, and that exogenous application of appropriate compounds may in fact induce the reproductive stage in immature trees. Useful acceleration of sexual propagation could thus be effected.

The few examples which I have cited serve to illustrate that, as in other areas of forestry, basic research is an important component of the tree improvement process.

Fungitoxic Agents from Forest Fungi: Protection of Stored Wood Chips

In the final part of this paper, I should like to give a slightly more detailed account of some work from my own laboratory.

For a number of years it was my privilege to be associated with the late M.A. Stillwell in a joint study whose objective was to use modified biological control techniques in combatting microorganisms associated with tree diseases or with deterioration of stored wood or wood products. Besides *Ceratocystis ulmi*, the fungus causing Dutch elm disease, the target organisms of particular interest to us were those responsible for stain and decay of stored wood chips.

It is often necessary for pulpmills to maintain large inventories of wood chips in storage for periods of several months, because of fluctuating supplies and markets. During such extended storage the action of fungi and bacteria on the chips takes its toll, in the form of discoloration and reduced fiber quality.

The fate of stored wood chips is graphically described in a recent publication by Shields (Eastern Forest Products Laboratory Bulletin).

> "Deterioration of chips begins as soon as a pile is built. Temperatures within a pile increase rapidly in the first few days. Initially this heat results from respiration of living wood cells and oxidation. This changes the chemical composition of wood extractives. In addition, fungi grow prolifically within a pile at this same time, creating more heat which contributes to the rapid increase in temperature in the large insulated chip pile mass. This warmer environment encourages growth of other "heat-loving" fungi which replace some of the earlier fungi that are restricted as the temperature rises above 40°C. Temperatures of 50 to 60°C and higher are found in large chip piles, and temperatures over 80°C, close to spontaneous combustion level, have been recorded.
>
> The upward movement of hot moist air within a pile produces a "chimney-effect" and can result in steam appearing at the top of the pile on a cold day. Temperatures above 65°C kill virtually all fungi in a pile. However, many "heat-loving" fungi can grow profusely in warm moist chips at temperatures up to 65°C. Some loss of wood substance can occur under

> the latter conditions, caused by those fungi which attack wood cellulose in the stored chips. An average weight loss of 1% per month of storage can be expected and losses up to 2% per month have occurred in some hardwood chips."

While several methods are available to ameliorate these problems including the use of small chip piles, first-on first-off processing, water sprinkling and chemical treatments, the pulp and paper industry still suffers substantial economic losses as a result of deterioration of stored wood chips, and the need for improved, environmentally acceptable methods to minimize these losses is recognized.

An attractive approach to the control of the wood-rotting and staining microorganisms affecting stored wood chips was conceived by Merlyn Stillwell, a tree pathologist at the Maritimes Forest Research Centre. In the course of studies on birch die-back disease, he had isolated from decayed yellow birch, *Betula alleghaniensis* Britt., an imperfect fungus, *Cryptosporiopsis* sp. which strongly inhibited the growth of other microorganisms (Stillwell 1966). Stillwell proposed that inoculation of a chip-pile with such a fungus, not itself a harmful wood-destroyer, could afford protection to the chips by inhibiting the establishment of the stain and decay organisms.

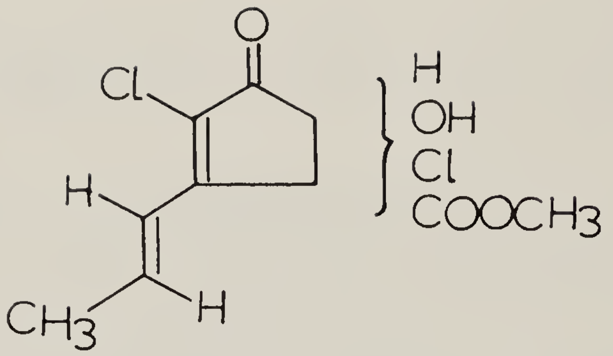
Studies conducted with a view to discovering the agent(s) responsible for the antagonism of *Cryptosporiopsis* sp. to other microorganisms led to the isolation of a crystalline fungitoxic metabolite from liquid culture medium which had supported growth of the fungus (Stillwell et al. 1969). This antibiotic, designated cryptosporiopsin, inhibited the growth of a broad spectrum of fungi, including many of those associated with stain and decay in wood-chip piles. On the basis of circumstantial evidence, it may be conjectured that cryptosporiopsin is at least partially responsible for the in vivo antagonism of *Cryptosporiopsis* sp. towards other organisms on a wood substrate (Stillwell 1966) but this has not been rigorously established.

In the context of the biological control strategy envisaged for protection of wood chips, pretreatment of the chips with a dilute solution of cryptosporiopsin prior to inoculation with *Cryptosporiopsis* sp. might assist the latter to become established on the substrate by reducing the population of competing microorganisms.

Chemical, spectroscopic, and X-ray methods were used in elucidating the molecular structure of cryptosporiopsin (McGahren et al. 1969; Strunz et al. 1969). The elemental composition of the substance was shown to be $C_{10}H_{10}O_4C1_2$. Spectroscopic and other evidence suggested that the molecule could be represented by the partial structure I (Fig 10). Location of the point of attachment of the methyl ester group established the complete carbon framework of the molecule. This was accomplished by a two-stage reduction of cryptosporiopsin to the cyclopentanone derivative II, which was rigorously identified by comparison with a synthetic sample.

The remaining structural problem, that of placing the hydroxyl group and chlorine atom, was solved (after an initial erroneous assignment based on misleading evidence) by reductive removal of the latter atom through the agency of zinc in methanol. The product had spectroscopic properties which indicated structure III, proving that the zinc-labile chlorine was located on C-5, hence that cryptosporiopsin is represented by structure IV. The antibiotic was found to be identical with a metabolite of *Sporormia affinis*, investigated simultaneously in an independent study by researchers at Lederle Laboratories (McGahren et al. 1969). The Lederle group used chemical and spectroscopic evidence, and X-ray crystallography to assign the structure and absolute configuration V to the metabolite.

The potential value of cryptosporiopsin, not just in the context of wood-chip pro-



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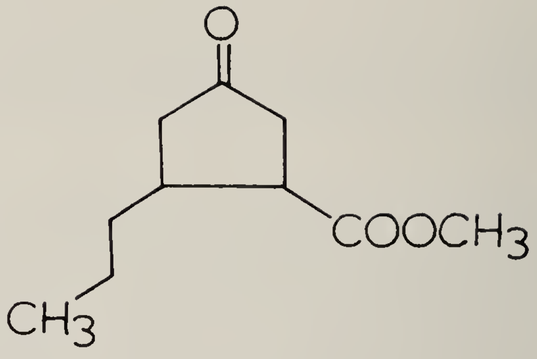

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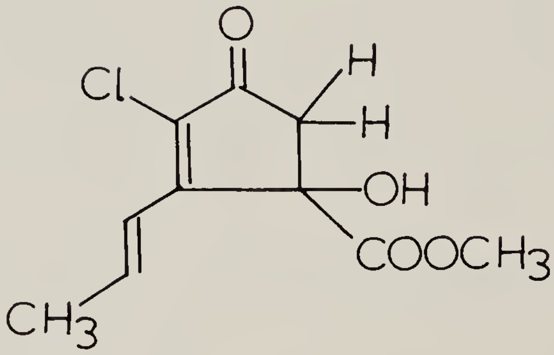
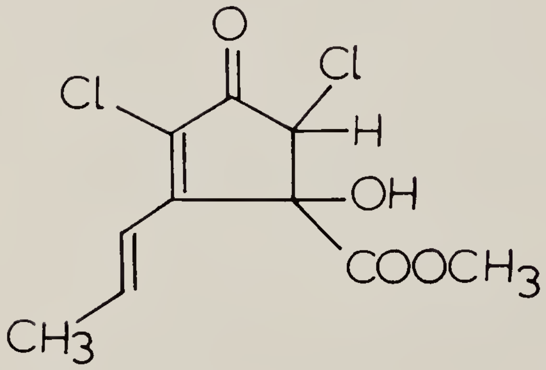
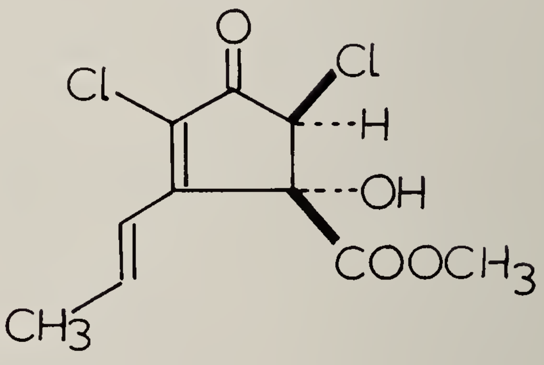


III

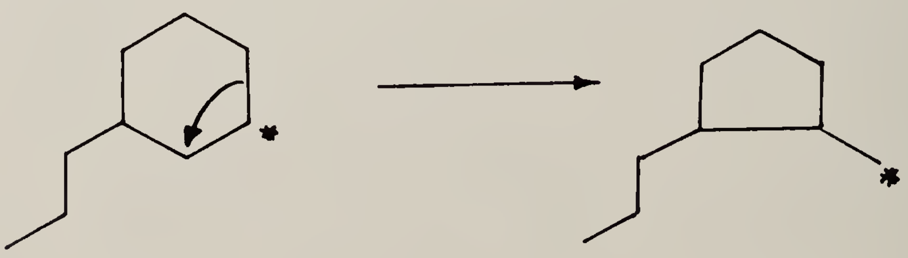


IV



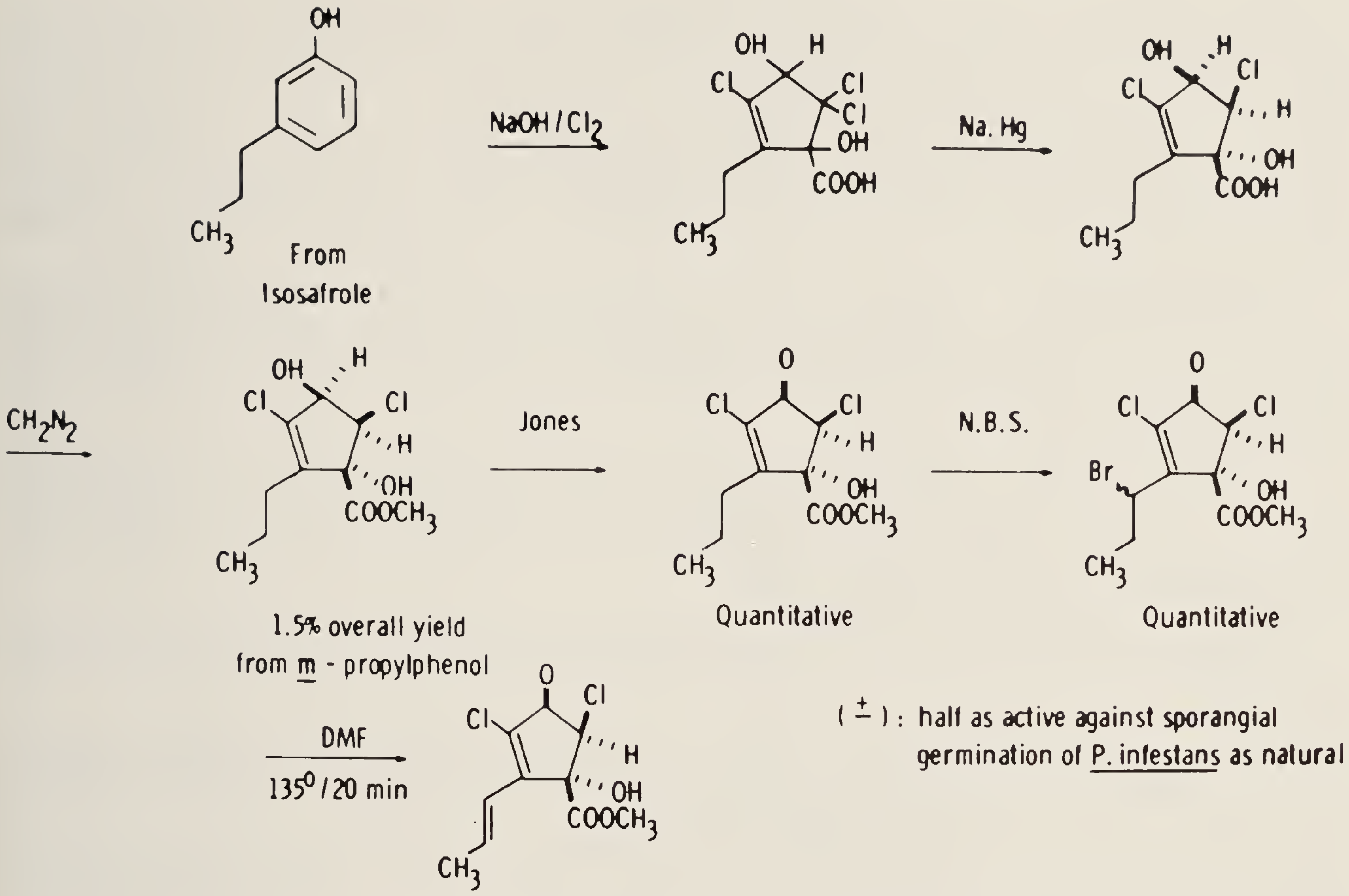
V

Fig 10 Structure of cryptosporiopsin (IV, V) and partial structures (I, II, III).



VI VII

Fig 11 Contraction of a functionalized 6-membered ring to 5-carbon cyclic structure.


From Isosafrole
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1.5% overall yield from m - propylphenol
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Quantitative
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135° / 20 min
(±) : half as active against sporangial germination of P. infestans as natural

Fig 12 Synthesis of cryptosporiopsin.

tection, but in other areas including agriculture, possibly even medicine, provided impetus for research into production of the antibiotic by chemical synthesis. Development of a viable synthetic pathway to this small, richly functionalized molecule resulted (Strunz & Court 1973).

Central to the synthetic strategy was a reaction, discovered almost a century ago (Hantzsch 1887; 1889), which effected contraction of a suitably functionalized 6-membered ring to a 5-carbon cyclic structure, depicted schematically as the transformation VI to VII (Fig 11). This strategy parallels the biosynthetic pathway through which the metabolite is formed in nature. The synthesis is shown in detail in Fig 12.

The chemical synthesis, while less efficient and economical than the biological production of cryptosporiopsin, opens the way to studies on analogues of the antibiotic.

While the chemical work on cryptosporiopsin was proceeding, Stillwell was actively investigating the antifungal spectrum and biological properties of the organism and its interesting metabolite (Stillwell et al. 1969; Stillwell, unpubl.).

He did not neglect the potential practical application of *Cryptosporiopsis* sp. in protection of stored wood chips, and a collaborative study in this area was initiated with W.H. Whitney at the Fraser Company mill in Atholville, N.B.

In a typical pilot-plant scale experiment conducted by these investigators, chips contained in nylon mesh bags (ca 20 lb/bag green weight) were sprinkled with a suspension of *Cryptosporiopsis* sp. mycelium, or moistened with an aqueous solution of cryptosporiopsin (0.5-1.0 mg/ml). Control samples, stored under the same conditions were untreated. The temperature in the middle of the samples was periodically monitored. A second group of control samples was stored frozen.

At the end of the test period (6-12 mo) the chips were processed, and the properties of the chips and the pulp prepared from the 4 groups of samples were assessed. Early results were promising, apparently indicating that pulp from the antibiotic-treated chips was only slightly inferior to that from the frozen samples, and somewhat better than pulp from chips inoculated with *Cryptosporiopsis* sp. Both treatments afforded pulp of substantially higher quality than the untreated controls (Stillwell, unpubl.).

With these results as encouragement, additional tests were planned by Stillwell and Whitney, but these had to be abandoned because of a reorganization at the Fraser Company which resulted in the closing of the research facility and pilot plant at Atholville.

In 1970-71, further pilot-plant studies were organized with the enthusiastic cooperation of R.T. Thaxter and others at the Great Northern Paper Company. The initial experiments in Millinocket apparently substantiated by and large, the results obtained earlier in the Atholville study.

Subsequent attempts to reproduce these successful treatments failed however, and further research is necessary to determine and eliminate the source of these erratic results.

In the meanwhile, other fungi were screened by Stillwell for fungitoxic effects. Several promising organisms were selected on the basis of their antagonism to other microorganisms. Two of these fungi, *Scytalidium* sp. and *Hyalodendron* sp., received particular attention in our laboratory on account of their interesting fungitoxic metabolites scytalidin (Stillwell et al. 1973; Strunz et al. 1972) and hyalodendrin (Stillwell et al. 1974; Strunz et al. 1973).

On the chemical front, the structural puzzle presented by scytalidin was solved largely by careful analysis of its spectra, as well as by controlled oxidative degradations to the small readily identified fragments VIII, IX, and X. From the accumulated evidence the structure XI was deduced for scytalidin (Fig 13). It is a bis-anhydride, related structurally and biosynthetically to the nonadride metabolites glauconic, glaucanic, and byssochlamic acids, and the rubratoxins (references in Strunz et al. 1972). The biosynthesis of scytalidin appears to be closely analogous to that proposed for byssochlamic acid (references in Strunz et al. 1972), and accordingly can be considered to involve the coupling of 2-C_{11} units possessing identical carbon skeletons at the appropriate oxidation level. The C_{11} precursor may be derived from the condensation product of an octanoic acid derivative with oxaloacetate, a citric acid cycle intermediate (Fig 14).

The molecular structure of hyalodendrin XII (Fig 15), like those of the other metabolites was elucidated by a combination of spectroscopic and chemical methods (Strunz et al. 1973). It could be converted chemically to the tetrasulfide XIII or the di-methylthio ether XIV, both of which (Fig 15), were isolated as its cometabolites from culture filtrates of *Hyalodendron* sp. (Strunz et al. 1975; Strunz et al. 1973). It is of interest to note that scientists at Lilly Research Laboratories in an independent study have isolated compounds enantiomeric with hyalodendrin and its congeners from fermentations of *Penicillium turbatum*. Similarly these compounds have been produced by an unidentified fungus NRRL 3888 at Abbott laboratories (references in Strunz et al. 1975).

Hyalodendrin is the simplest member so far isolated of the growing class of epidithiodioxopiperazine metabolites comprising, inter alia, gliotoxin, the sporidesmins, the aranotins, chaetocin, and verticillin A (references in Strunz et al. 1973).

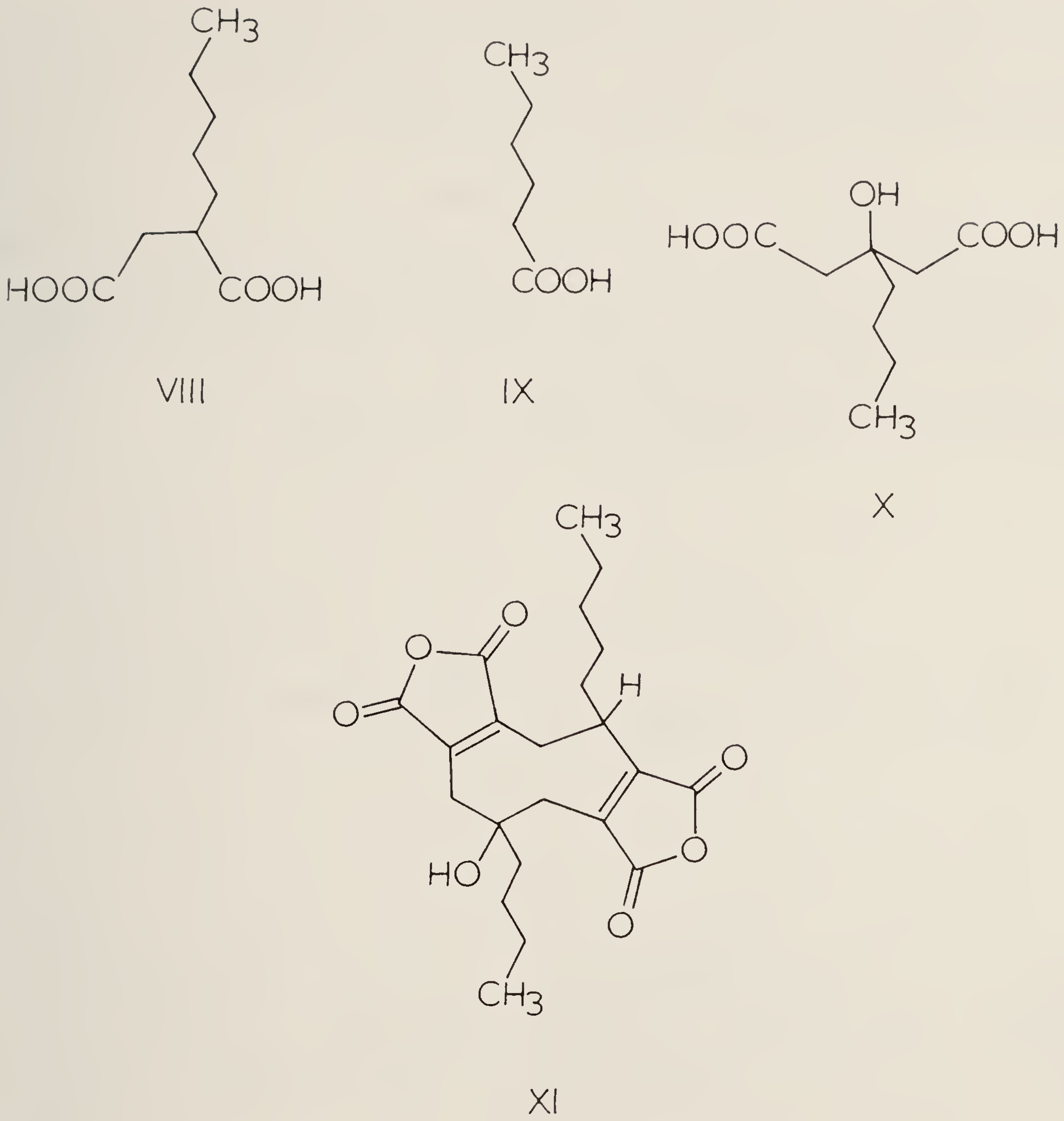


Fig 13 Structure of scytalidin (XI) and fragments (VIII, IX, X).

A chemical synthesis of hyalodendrin in our laboratory followed the ingeneous strategy developed by Y. Kishi in his synthesis of dehydrogliotoxin and members of the sporidesmin family (Strunz & Kakushima 1974, and references therein). A key intermediate (Fig 15) in this approach is the thioacetal XV (R = $CH_3OC_6H_4$), a protected precursor of the epidithiodioxopiperazine ring. Sequential alkylation reactions are used to add the benzyl and protected hydroxymethel functionality, and subsequent manipulations lead to racemic hyalodendrin. A simplified route to epidithiodioxopiperazines was later developed by Kishi and applied in a second synthesis of hyalodendrin (Fukuyama et al. 1976).

Interesting biological properties, including antifungal, antibacterial, antiviral, and cytotoxic effects have been found to be associated with various members of the class of epidithiodioxopiperazines (references in Strunz et al. 1973). While hyalodendrin was subjected to limited testing for protection of wood chips, its lack of solubility in water and its considerable mammalian toxicity will probably preclude its further development.

The untimely death of Merlyn Stillwell in 1977 has left the wood-chip study in our laboratory incomplete. The use of biological control methods to combat tree pathogens and organisms associated with wood decay remains an exciting possibility which continues to be explored in other laboratories.

Conclusions

The practical problems of forestry call for research in a number of scientific disciplines in order to develop all possible methods of dealing with them.

The ultimate objective is to integrate these methods into forest management plans, and their value should be assessed in terms of their long-term effects on the productivity of complex forest ecosystems.

Applied research and fundamental research are indivisible!

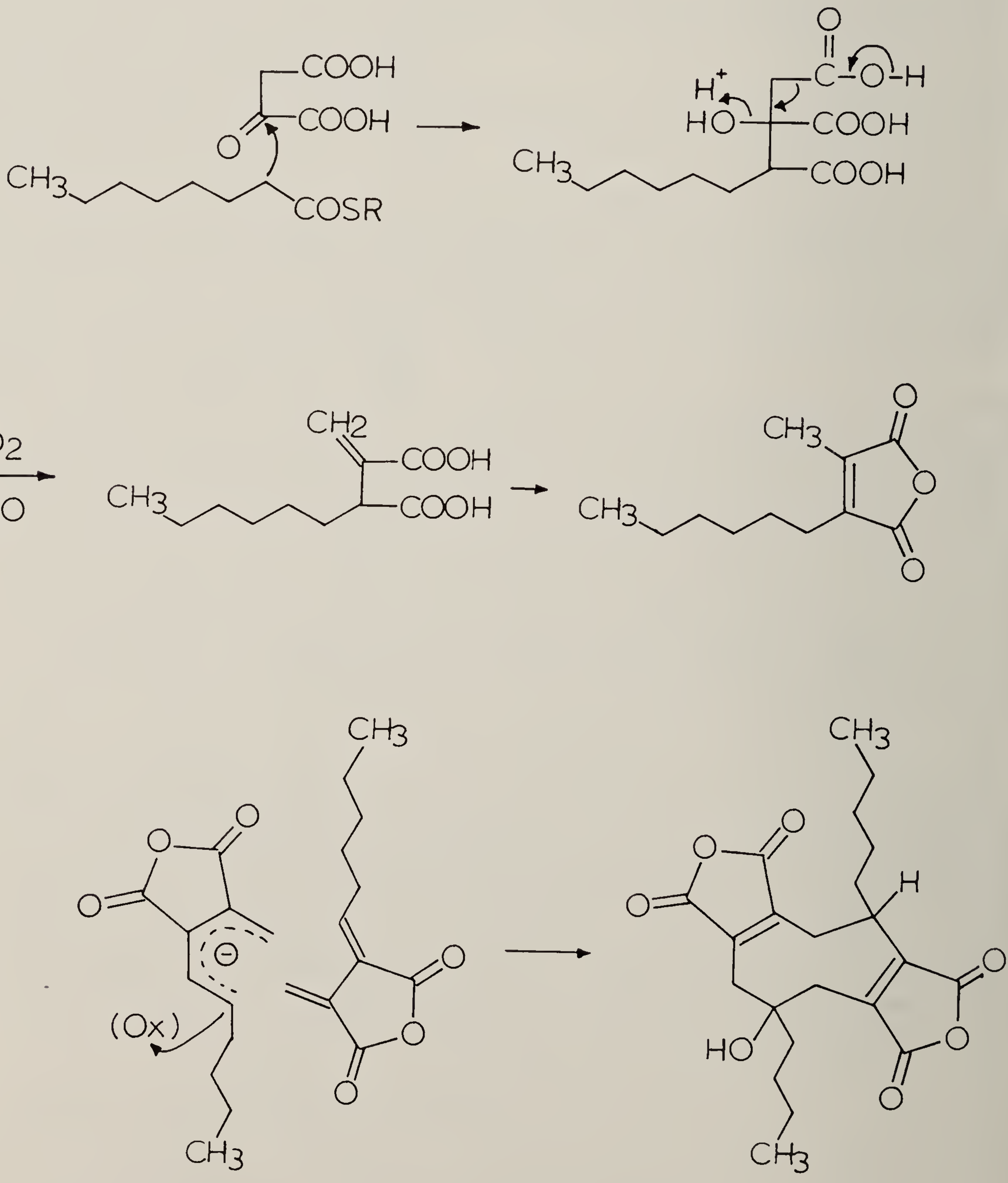
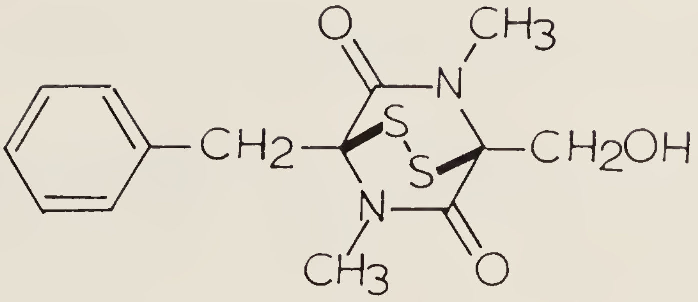
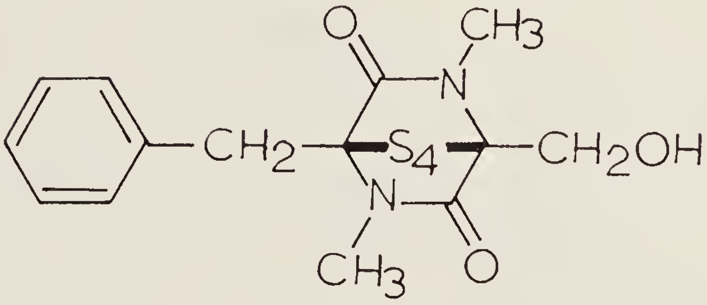


Fig 14 Biosynthesis of scytalidin

XII



XIII



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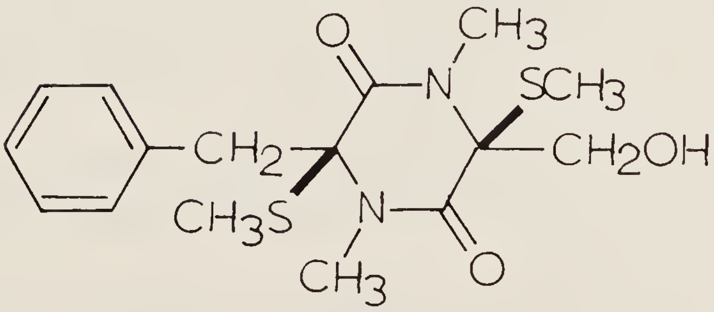

XV

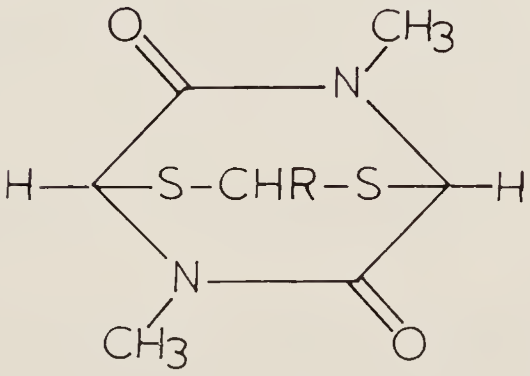

Fig 15 Structure of hyalodendrin and related compounds

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Special thanks are extended to R.E. Balch, who read the manuscript and made a number of very helpful comments and suggestions.

In the chemical work discussed in the latter part of the paper, I enjoyed the valuable collaboration of several co-workers whose names appear in the references.

Finally, I would like to pay tribute to the memory of Merlyn Stillwell, a stimulating colleague and good friend for more than 10 years.

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AGRICULTURAL RESEARCH AND DEVELOPMENT IN ATLANTIC CANADA

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The status of the agricultural industry in Canada is summarised and the segment of the industry in the Maritime Provinces reviewed in its relationship to the whole. The level of research and development in the industry in the Maritime Provinces is examined in detail, and it is concluded that an increase in such activity is desirable. Areas that require greater investment in research and development are presented.

Introduction

Agriculture in Atlantic Canada generates farm-cash receipts of approximately $400 million annually and with value added, the sector grosses in excess of $600 million in total revenues. Farmers in the region, aided by government, are oriented toward growth. Under the aegis of the Maritime Farmers Council, a product of the 3 Maritime Federations of Agriculture, producers have set for themselves the target of tripling the size of the agricultural industry in the region by the early 1990's. This initiative, which was effectively launched in late summer of 1979 within the framework of "The Billion Dollar Challenge", has given a sense of purpose and direction to this industry at the very level where the action is centered and where the development must ultimately begin, i.e. on farm and among producers. But let us examine more carefully some of the trends and indicators within the agricultural sector as a basis for reflection on future research and development initiatives.

Canadian agriculture generates in excess of $10 billion annually in farm cash receipts (Table I), 52% of which is derived from the sale of livestock and their related products and the balance (48%) accrues from the production of a diverse array of crop plants.

The 3 Maritime Provinces contribute about 3% of this total from 4% of Canada's census farms. Livestock in this region commands a proportionately greater share of attention than the national whole, accounting for approximately two-thirds of the total farm receipts.

Some measure of the extent to which Atlantic agricultural potentials are currently developed can be obtained by relating the extent of present farming to the total land area which is considered suitable for agriculture, as classified according to the Canada Land Inventory, classes 1 to 6 inclusive. Canada's food-land resource totals about 122 million hectares (Table II). If we assume that the bulk of the present farms are already located on land that falls within this same class range, then a surprising 56% of the adapted whole is currently utilized, ranging from a high of 84% in Saskatchewan to less than 1% in Newfoundland. Looking specifically at the Maritime Provinces, one is not surprised to find that Prince Edward Island has the highest rate of suitable land already committed to agricultural purposes, followed by Nova Scotia where there is potential for a near tripling of actively farmed lands and finally, New Brunswick which, with its relatively low level of utilization for agricultural purposes, appears almost as a development frontier.

The great bulk of the potential agricultural land is class 3 or lower, i.e., the soils have distinct limitations such as in fertility, organic matter content, moisture, etc.; nonetheless there is sufficient adapted land to support significant growth within the sector (Table III).

Table I. Farm-cash receipts (1977) for Canadian agriculture

	Thousands of Dollars
Nova Scotia	127,000
New Brunswick	109,000
Prince Edward Island	88,500
Quebec	1,430,000
Ontario	2,860,000
Manitoba	899,000
Saskatchewan	2,140,000
Alberta	1,990,000
British Columbia	502,000
Canada	10,100,000

Table II. Utilization levels for agricultural land in Canada (hectares x 1000)

	Total Farmland	Potential Agricultural Land	Percentage Utilization
Newfoundland	25	3,306	1
Prince Edward Island	309	523	59
Nova Scotia	529	1,650	32
New Brunswick	538	5,000	11
Quebec	4,288	6,390	67
Ontario	6,441	12,815	50
Manitoba	7,591	11,710	65
Saskatchewan	26,016	31,153	84
Alberta	19,814	39,649	50
British Columbia	2,318	14,570	16
Canada	67,734	121,766	56

Agriculture in Canada has enjoyed relatively steady growth in spite of a continued consolidation in the resources (land and labor) used in food production. The development record over the period 1961-76 has in fact been a very creditable, 3.5% growth per year in indexed dollars (Table IV).

Comparable figures for the Maritime Provinces for the same period, however, show an average growth in real-farm cash receipts of 1.2%/annum for Nova Scotia; 2.9% for Prince Edward Island, and zero growth for New Brunswick. If the current growth rate only is sustained, we will experience only 15% growth overall by 1990 or about 60 million indexed dollars. On the other hand, Maritime ingenuity and drive in concert with a significant developmental impetus within the sector could result in a farm-gate value of $600 million or 50% growth over the next decade. If so, then the balance of the billion dollars sought in the "Challenge" will have to come from ad-

Table III. Potential agricultural land by soil capability, class and province, Canada, 1971 (hectares x 1000)

Soil Capability Class	B.C.	Alta.	Sask.	Man.	Ont.	Que.	Atlantic Provinces	Canada
1	70	831	1,072	184	2,249	14		4,402
2	398	4,041	6,446	2,556	2,360	976	611	17,388
3	1,000	6,477	10,082	2,190	3,279	1,381	2,561	26,940
4	2,132	9,940	4,252	2,573	2,902	2,830	2,544	27,173
5	6,138*	11,433	7,799	2,250	1,910	1,636	2,352	33,518
6	5,358*	3,794	4,065	2,162	1,192	9	2,903	19,483
Total	15,096	36,486	33,716	11,915	13,892	6,846	10,971	128,904

*Incomplete

Sources: (1) Canada Land Inventory, Soil Capability.
(2) British Columbia Environmental Land Use Commission Victoria, B.C.

Table IV. Historical performance of the Canadian food industry

	Real Domestic Product: By Sector		
	Agriculture	Fisheries	Food Processing
1961	100.0	100.0	100.0
1964	123.9	110.9	117.9
1967	118.6	115.6	136.8
1970	131.4	119.7	149.3
1973	142.3	104.1	166.9
1976	153.3	N/A	173.5

* Indexed measure of output in constant 1961 dollars.
Source: Statistics Canada publications, catalogue 61-005 (March 1974 supplement) and 61-510.

ding value to the sector through more complete processing and product manufacture from the base agricultural products of the region.

Some added insight to development potentials can be obtained if one compares present returns per hectare of land farmed from province to province across Canada (Table V).

Although a very coarse input/output measure, the average rate of return per hectare committed to both crop and livestock enterprises exceeds the national average but falls substantially short of Quebec and particularly Ontario which have a similar sort of agriculture to the Maritimes. Again Prince Edward Island appears to derive

Table V. Cash receipts per hectare of land farmed in Canada, 1977

	Total Farm Enterprise	Crop Receipts Only
Newfoundland	*	*
Prince Edward Island	286	132
Nova Scotia	240	51
New Brunswick	203	81
Quebec	333	31
Ontario	444	146
Manitoba	250	64
Saskatchewan	82	63
Alberta	100	50
British Columbia	217	72
Canada	149	65

*Not available

the highest level of return from its present foodland resource whereas, New Brunswick is on the low side among the 3 Maritime Provinces. These data do suggest: (1) the importance of stressing commodities which can be grown to comparative advantages with potential for maximum returns; and (2) there is a need and an opportunity to increase efficiency in relation to the output from the basic units of adapted agricultural land. I project that better utilization of existing resources alone would add nearly $300 million annually to the Maritime farm total.

Certainly the point I wish to make is simply that the "Billion Dollar Challenge" target is attainable even within the time frame set by its principals. If this goal is to be achieved, however, Maritime farmers as a whole must become more innovative and oriented toward sector growth. Most importantly, they should strive for even higher levels of returns from their base land, labor and material resources inputs through the employment of even more effective production and marketing approaches.

Agricultural Research

The challenge to the agricultural researchers flows quite naturally from the foregoing. As I see it, the role is primarily one of enhancing the comparative advantage for food production in Atlantic Canada by identifying those commodities which the region might produce to advantage and secondly, developing the appropriate technology to enable regional producers to fully exploit their apparent advantage. There is a responsibility also, which is jointly borne by industry and government, to ensure consumers in Atlantic Canada of a safe, well-balanced or nutritious diet of foodstuffs at reasonable prices and in reliable supply. This suggests continued production of certain commodities which may not be grown locally to any comparative advantage but which through problems of transport, supply, and perishability would be scarce and more costly were it not for the commitment of local producers. These same commodities, and the dairy sector is a good example, often require some level of public subsidy to ensure adequate returns to the producers and here also, there is significant responsibility on the scientist and the farmer to develop and employ a level of technology which minimizes the subsidization demands of the sector.

Let us look then at agricultural research as it is practiced both nationally and regionally. And because this sector is so integrally interwoven with the social and economic fabric of Canada, we should identify at least some of the major current issues and challenges.

Resources

It is difficult to provide a highly accurate description of the resources allocation to agricultural research. However, because of the sheer size of the sector we can tolerate a fair amount of error and still arrive at a fairly thorough overview.

Total expenditures on food and agricultural research (Table VI) in 1978-79 approximated $263 million. And the largest single research component, or 51%, is represented in the R & D activities of Agriculture Canada with its professional staff of about 937 scientists dispersed among 55 establishments from coast to coast. Universities, we estimate, commit an additional 520 full time person-years or about 30% of the national effort. Industry selectively employs another 140 scientists, largely in the food research and plant breeding fields; and the National Research Council through its network of laboratories devotes about 46 person-years of professional R & D support to the food and agriculture sector.

The adequacy of this level of commitment can be assessed in several ways. On the one hand, expenditures can be related to the gross returns, i.e., overall economic

Table VI. Resource allocation for agriculture and food research, 1978-79

Agriculture Canada	$134.7 million
Fisheries and Environment	38.0 million
N.R.C.	10.7 million
Universities	57.2 million
Provinces	9.6 million
Industry	12.5 million
	$262.7 million

impact of the sector. Excluding imports, the food and agriculture producers of Canada, consisting of farmers and processors, must gross something in the order of $25 billion annually. Conventional wisdom has dictated that a 2% R & D investment is of the right order of magnitude which, if applied, would dictate annual expenditures of about $500 million to food and agricultural research. Clearly the present $275-300 million is nearer the 1% level and about half-strength if judged by this yardstick.

Adequacy might better be judged however in terms of the principals in the food system serviced by this research community, i.e., the farmers at the one end of the chain and consumers at the other. In short, can we relate with the clientele and draw some appropriate conclusions?

Table IV shows that in spite of a massive 50% consolidation in farm numbers over the past 30 years and a 25% reduction in designated farmland, there has been steady growth in the real output of the farm sector as it has been in the order of 3-4% per annum over the past 2 decades. Most significantly the growth rate has exceeded the 2%/year cited for the United States agriculture, although the measure of reference is for a significantly longer period of time. Farming generally in this counry is, I believe, in a reasonably healthy state and I share the view of persons like Wortman (1979) that science as well as industry have effectively provided the building blocks for the relatively advanced agricultural systems which make up Canadian agriculture.

And the Canadian consumer appears fairly treated as well. The proportion of income spent on food has declined progressively over the past 20 years to less than 20% of disposable incomes although inflation has somewhat reversed this trend lately. Nonetheless Canadian food costs are either the lowest or certainly among the lowest in the world, and this too is a tribute to those who labor within the Canadian food system as well as to the level of technology which they employ.

These 2 indicators, at least, suggest that the sector is reasonably well-attended. I accept also that higher order R & D inputs are likely to further stimulate real agricultural growth as well as to give additional advantage to the consumer. But the basic question of adequacy can, it seems to me, be responded to affirmatively. What may be more to the point, however, is the adequacy of the distribution and the regional health of the food and agricultural research effort.

Again, recalling earlier-cited statistics, real growth of Maritime agriculture has been averaging only about 40% of the national growth rate. Does this relate in any way to the relative extent of R & D supports?

It is true that in the absence of any agricultural faculties at Atlantic universities, this significant source of expertise is relatively underdeveloped in the region. Most recently we see signs of encouraging developments in this direction at the Nova Scotia Agricultural College in relation to the basic agricultural sciences and similarly, there are healthy indications of new initiatives in food research.

The provincial Departments of Agriculture in Atlantic Canada have not developed any extent of R & D programs. Instead, with their own constraints on resources, they have chosen to support and complement the federal Research Stations within the region by transferring and extending new technologies to the farm level.

Federal science managers would probably insist that budgets and related resource allocations to the region are equitable as the present $12 million allocation to the existent federal institutions represents about 4.5% of the total Canadian agricultural research budget and that equates very favorably with the approximate 4% gross output of the region.

Such an attitude ensures, however, only the status quo and surely militates against future growth in the regional sector. The facts are that the region includes 9% of Canada's foodland resource, 10% of its people, and moreover, its farmers have said that even in today's economic terms, a reasonable target for total farm gate returns would be $1 billion or again, 10% of Canada's gross farm output. Clearly, if the Atlantic Region is to break out of its historical performance bounds, the scale of research investment should be in the order of a doubling of present R & D commitments to the sector.

Such stimulus would not only enable the proper franchise of the Agriculture Canada Research Stations to service the commodity development interests but would in addition encourage a significant commitment of university and industrial researchers in the region to food and agricultural research.

The Program

Considering the great diversity in crop and livestock enterprises as well as the complexity of the food system itself, any initiatives to generalize on program would seem relatively futile. On the other hand, there is just enough commonality to allow one to identify several recurring elements.

Resources development or the concept of more efficient utilization of existing natural soil, water, and climate resources is a logical beginning point. In spite of the fact that our soil resource has been systematically mapped and classified, I find very little information which can be used to determine the suitability of our Atlantic soils for production of the various existent and potential crop species. Nor do development initiatives selectively differentiate and stimulate crop production according to any philosophy based on a "best use" concept. The consequence is under-utilization of the based soil resource and so we find some of our best class 2 land given over to pasture while at the other extreme, fruit growers are attempting to develop highly productive orchards on land which should be pastured.

Even given adequate inventory and suitability data, we need many more technological developments to enable a fuller exploitation of the soil resource. Agricultural soils in the Atlantic region are generally acid, low in fertility and organic matter content, imperfectly drained, and inundated with physical or structural problems, both natural and man-made.

Water, in a maritime environment would seem invariably to be a natural resource in excess supply yet on the lighter soils and particularly with the production of the relatively more intensively-cultured, high value crops, significant drought stresses and loss in productivity will usually occur one or more times throughout the growing season. We are generally lacking in appropriate irrigation technology.

Climate itself might seem at the outset to be beyond easy manipulation. Nonetheless, as we attempt to farm under relatively harsh conditions, it behooves us to develop ways and means which enable the manipulation or fuller exploitation of that which we have. To give examples of the sorts of technology which need stimulus let me cite; 1) the matter of windbreaks and hedgerows and their impact on plant and animal production and protection; and 2) protected culture and the use of plastics and other means to extend the growing season through the artificial creation of a suitable environment for plant growth.

Breeding and genetic manipulation is the next major component of agricultural R & D which warrants continued stimulus. Remarkable strides have already been achieved in quality and with output of everything from milk and eggs to gherkins and strawberries. Moreover, the base adaptation has been altered to the point where crops such as grain, corn, and soybeans, which simply could not be grown here 10 years ago are now part of the local agricultural scene.

Natural speciation and survival has contributed also to genetic variability for traits which govern tolerance to various economic diseases and insect pests. Often the lowest cost and most stable means for control has been delivered by the breeder and geneticist.

Much is said these days about plateaus and it may be that some of the early works will be the most dramatic. The following table (Table VII) illustrates something of the contrast between known potentials and average production based on 1974 statistics, and I have no doubt that many of these so-called records are being re-established at new, even higher levels.

The third major challenge is the *development of efficient production and protection technology* which would enable the full exploitation of the enlarged genetic potentials. The poultry industry with its factory-type operations most closely approaches the upper limits of performance of any of the commodities. Hog production follows next on the efficiency hierarchy and the key is most likely that a fairly well-defined and complete system of production has been put in place in both instances. Housing structures, optimum population size, diets, animal health programs, etc., have been well-elaborated in economic terms and recommendations consequently have become standardized. Even more important, producers have

Table VII. Average and record yields (Wittwer 1975)

Food	Average, 1974	Record
Corn (bu/acre)	72	307
Wheat (bu/acre)	28	216
Soybeans (bu/acre)	24	110
Sorghum (bu/acre)	45	320
Oats (bu/acre)	48	296
Barley (bu/acre)	38	212
Potatoes (bu/acre)	420	1400
Sugarbeets (ton/acre)	19	54
Milk prod'n/cow (10^3 lbs)	10	50
Eggs/hen	230	365

generally seen a better-than-average success ratio in these instances and are now looking for something similar with the other commodities.

Unfortunately, where climate, disease, or pest variables are relatively less stable, these base production systems are less-easily defined. Nonetheless some parameters can be stipulated to the advantage of producers and a reference point established to which one can begin to build with better understanding and manipulation of the components within the system.

Fourth and final among production-oriented programs is the need to develop *improved technology for the harvest, handling, and storage* of plant and animal products, not only to maximize output efficiency on farm, but also to assure improved quality and greater continuity of supply and hence, more efficient marketing technology overall.

The fifth major category of R & D effort to which I will refer is the so-called "P.D.R." or processing, distributing and retailing sector. It is the program area which selectively will experience significant growth over the decade of the 1980's as at present only about 8% of food and agricultural-research resources are committed to this sector. There is also an increasing awareness of the significant development impact which will acrue with more complete processing and preparation of foods from our raw products array.

Development of new products and improved processing and food manufacturing technologies constitute the 2 major research initiatives within the sector. I would look for leadership first from the industry itself, but there is also a continuing role for the governmental and university laboratories in support of the processors, both large and small.

The Issues

To conclude my remarks on agricultural research, I would propose to highlight just a few of the more significant issues which are very much a part of today's agriculture.

(1) *Credit costs and high capitalization.* The high cost of land, buildings, and machinery makes it increasingly difficult to attract new entrants into farming as a vocation. Moreover, the current high price of borrowed money required to provide operating capital, particularly for those commodities where there is a substantial lapse in time between planting and harvest is a major determent. Land assembly and extension of leasal arrangements to farm operators would ease the capital burden since about 75% of capitalization in farm enterprises is tied up in the land component. Similarly, programs already exist to enable advances in payment for certain crops and in this way assist the producer to bridge the interval from seeding time to the point where his crop can be marketed.

(2) *Mechanization* is an issue today with significant socio-economic ramifications. There is, as noted earlier, the high capital-cost burden associated with equipping many of today's modern farms. Appropriate machinery technology needs further research and stimulus to production, particularly as relates to Atlantic Canada since we have no local manufacturing base but rely instead primarily upon the United States technology which is geared to the west and the mid-west with their highly extensive type of farming.

An additional aspect of the mechanization issue is the growing opposition in the United States to the public funding of research aimed particularly at mechanization of the harvest operations. This has become a highly emotional matter and the labor movement with its basic job concerns appears to be gaining ground since Agriculture Secretary, Bergland has openly declared his opposition to continued funding of mechanization research and stated that private firms should be paying for these developments.

In an area such as Atlantic Canada where unemployment rates are relatively high, it seems incongruous to commit significantly to mechanization R & D. The consequences of not moving in this direction are serious however. Farm labor situations are simply least-choice options and without machine substitutions for labor, the competitive position of farmers will erode to the point where certain commodities can no longer be produced locally.

(3) *Chemical technology and particularly pesticide usage* is a matter of continuing concern to Canadians. All of us prefer our foods "au naturel" without chemical additives. Even as recent as January 30th, Agriculture Canada's Deputy-Minister, Gaétan Lussier, issued a formal statement on this issue:

"The Department's position is that the use of chemical pesticides is essential to efficient agricultural production and an abundant food supply. Pest-resistant varieties, integrated management techniques, cultural practices and biological control methods are the first line of defence against insects and weeds, but judicious use of pesticides is essential to modern agriculture. In other words, their use at the present time is necessary for maintaining an acceptable level of agricultural production. If viable and economical alternatives become available, Agriculture Canada will be the first to support their general use."

Clearly the importance of stimulating research to develop resistant varieties and alternative approaches to disease, insect and weed control cannot be overemphasized. The high development costs associated with new pesticides and the increasing restrictions and withdrawals by regulatory authorities serve only to make the overall situation more acute.

(4) *Energy*. Apart from the significant input production cost increases associated with rising fuel costs, there is growing interest in Canada in the feasibility of displacing hydrocarbon fuels with energy sources derived from agricultural crops. Alcohol fuels may offer feasible options according to Hayes and Timbers (1980) and major pilot production studies are currently underway in North America and other countries.

Basically, any substantial agricultural contribution to the national fuel requirement would require an extensive land base, suited to large-scale production of industrial crops. That does not sound very much like Atlantic Canada but more nearly describes Prairie agriculture to my view. On the other hand, however, significant quantities of waste or cull potatoes are available in the region and offer excellent substrate for small-scale "moonshine" or turnkey operations which could potentially service the fuel needs of relatively small groups of cooperating farmers. Similarly crop residues and wastes are available from local processing operations which might offer usable substrate. Engine technology, licensing, and distribution concerns will require some resolution prior to any widespread developments. Nevertheless energy production in association with Atlantic agriculture is worthy of further exploration.

DeWit (1979), from the Netherlands, has written recently on the greater issue of limited availability and increasing costs of energy sources and his conclusions are worth sharing. Not only is the issue one of fuel, for there is direct implication to the supply of chemical fertilizers and pesticides as well. He states:

> "If energy should become a very scarce resource, it would be possible to grow agricultural products without the use of yield-increasing inputs. This would lead to lower yields and would still result in an increase of the added energy use per unit product, unless the energy use for substitution of labour were minimized at the same time. It may be questioned whether the total production volume would then be large enough to cover the basic needs. It is, however, certain that under such circumstances all reclaimable soil would have to be taken into production and much labour would be needed on the farm; it would then be impossible to maintain the urban civilization we seem to like.
>
> However, although scarce, it seems likely that energy is available in at least reasonable quantities for a long time to come. In that case, agriculture may contribute to a sensible use of energy, by developing in a direction where as high yields per hectare as possible are obtained from as small an acreage as possible by a reasonable number of highly skilled farmers per hectare. The spin-off from increasing energy productivity by higher yields per hectare and some substitutions of energy by labour may be considerable:
>
> (i) less energy use per unit of product; (ii) greater need for skilled labour in a society where job opportunities are limited by automation; (iii) more land available for other purposes; (iv) reduction of the environmental impact of agriculture because less resources are used per unit product and then in a more confined area; (v) and last, but not least, a challenging task for the agricultural scientist."

This statement provides a good point at which to conclude my overview of Atlantic agricultural research. While I am of the opinion that the resources fall short of the developmental requirements for the sector in the region, I believe that the base orientation of the research has been in the right direction and that the achievements to date are already significant. Our future is surely vested in the degree to which we succeed in effectively utilizing our rather limited resources and in the extent to which we exploit the unique comparative advantages which the region does enjoy.

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RESEARCH AND DEVELOPMENT IN THE STEEL INDUSTRY IN NOVA SCOTIA*

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The world state of the art in ironmaking and steelmaking is examined, and an attempt is made to show where the present and future operations of the Sydney Steel Corp. fit into this world picture. Financial and political considerations are excluded from this examination. Examples are given of applied industrial and laboratory scale experiments, as well as fundamental investigations on chemical reactions important in steelmaking.

Introduction

Any attempt by one who is not employed in the industry to write authoritatively about it should be accompanied by some statement of one's bona fides. At the Atlantic Research Laboratory of the National Research Council we have been involved for 25 years in research on high temperature chemical reactions important in steelmaking. We have maintained close contact with developments at the Sydney Steel Corporation (SYSCO) and thus are generally familiar with the overall picture. We are part of the Atlantic Group for Research in Industrial Metallurgy (AGRIM), a cooperating group of metallurgical engineers and scientists at the Technical University of Nova Scotia, Nova Scotia Research Foundation Corporation, Dalhousie University, College of Cape Breton, the Cape Breton Development Corporation, and SYSCO. Some of the work which I will describe was sponsored by this group.

I intend to restrict this paper to aspects of steel production, and in order to define this more closely let me mention a few things I am not going to discuss. First of all I am not going to touch on the technology of steel fabrication, although it is obvious that our modern society will continue to benefit from research and development of new alloys for special applications. Very high strength steels, with the subsequent reduction in weight that they allow, are becoming more important. They bring with them serious problems such as fatigue failure and stress corrosion failure. Therefore research on heat-treating, machining, welding, corrosion, strength, etc., is being done all over the world in the fields of physical metallurgy, mechanical engineering, metal physics, and others. Such research may well be very important to Nova Scotia if we become, as some predict, technically sophisticated in such areas as ocean engineering. The Nova Scotia Research Foundation and Technical University of Nova Scotia are examples of local research institutes with clear interests in such areas. However, I suggest that the industry with which such efforts are related is manufacturing, rather than the basic steel industry, and so I will not discuss them further.

Really, what we are left with to discuss is SYSCO as the present basic industry, and investigations into the extractive metallurgy of iron and steelmaking as the research. Of course, we all know that economic and political implications underlie the technological side of this industry in Nova Scotia. It seems fairly obvious that even a technologically modern steel plant would find it difficult to turn a profit under the burden of debt now attached to SYSCO, and so the continued existence of SYSCO appears to require favorable political decisions. In such a situation, for example, it could well be that a substantial effort should be devoted to research into various political methods of reducing SYSCO's capital debt load; this might pay better dividends than research into better ways of making steel. However, we must attempt here to stay away from such considerations. There are a number of papers on the economics of the industry, many in connection with the late CANSTEEL project, and one such background paper that can be recommended is titled "Steelmaking in the Atlantic Provinces" (1974). It was prepared by Atlantic Provinces Economic Council in 1974 and still is relevant.

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*NRCC No. 18617

My paper, then, is about the technology of steelmaking, and it is in 2 parts. The first is an examination of the world state of the art in ironmaking and steelmaking, with an attempt to show where the present and future SYSCO operation fits. The second is a look at some current local research, including industrial scale programs and fundamental laboratory studies.

World Steel Production

In 1978 world steel production was about 540,000,000 tonnes, with roughly 25% contributed by each of western Europe, eastern Europe plus USSR, North America, and Asia. In total, the western world produces 66% of the world's steel. Canada makes a considerable contribution, 2.1% in 1978, up from the 1.9% of 10 years ago. In 1980, when the current round of expansion of STELCO, DOFASCO and ALGOMA is finished, Canada's percentage will be approaching 3%. The 1978 production amounts to some 11,000,000 tonnes of steel and of this Nova Scotia makes between 0.5 and 1 million tonnes. Thus Nova Scotia makes between 0.1 and 0.2% of the world's steel.

To put the world's steel production in a somewhat more scientific context, we may calculate that the rate of production of new iron (not counting recycled scrap) is about 2.4×10^5 moles/sec. This is a very large number when we realize that laboratory experiments are usually on the scale of millimoles or micromoles per second.

The production of steel is a basic indicator of the industrialization of a country, and is often a source of national pride. Table I shows the per capita steel production

Table I. Per capita production of steel for selected countries

Country	Tonnes per capita*
Luxemburg	14.2
Belgium, Czechoslovakia, Japan	1.3-1.0
Canada, W. Germany, United States, USSR, Poland, Austria	0.7-0.6
Sweden, Italy, France, United Kingdom, E. Germany	0.5-0.4
Taiwan, Korea	0.2
China, India	0.04-0.02

*Steel production is for 1978, populations are for 1971 of some arbitrarily chosen countries. Canada places well up among industrialized countries and in 1980 might rank with Japan. It is interesting to note that a plant of the size of SYSCO just about maintains the Atlantic provinces in line with the 0.5 - 0.7 tonnes/person/year figure.

Let us examine the technological state of the art. The overall process essentially is comprised of two steps: (1) ironmaking, followed by (2) steelmaking. Ironmaking is the reduction of iron ore, largely Fe_2O_3, to a solid or liquid metallized product which contains 5 or 6% of impurities of one sort or another. Steelmaking is refining this crude product into a material of the correct chemical and physical properties to meet a customer's specifications. We do not make as much new iron as the steel production figures would indicate because of the recycling of scrap.

Ironmaking

Blast Furnace

Over 95% of the world's iron is produced in blast furnaces. These are tall stack furnaces where solids (ore, coke, and limestone) are put in at the top and liquids are taken out at the bottom on a more or less continuous basis. Figure 1 shows a typical configuration. Pre-heated air is forced in at the bottom and converts coke to CO, the heat of the reaction raising the temperature to 1500°C at which temperature CO can reduce the oxide to iron. Impurities in the ore, largely silicon, are combined with limestone as they are liberated to form a liquid slag. The characteristics of blast fur-

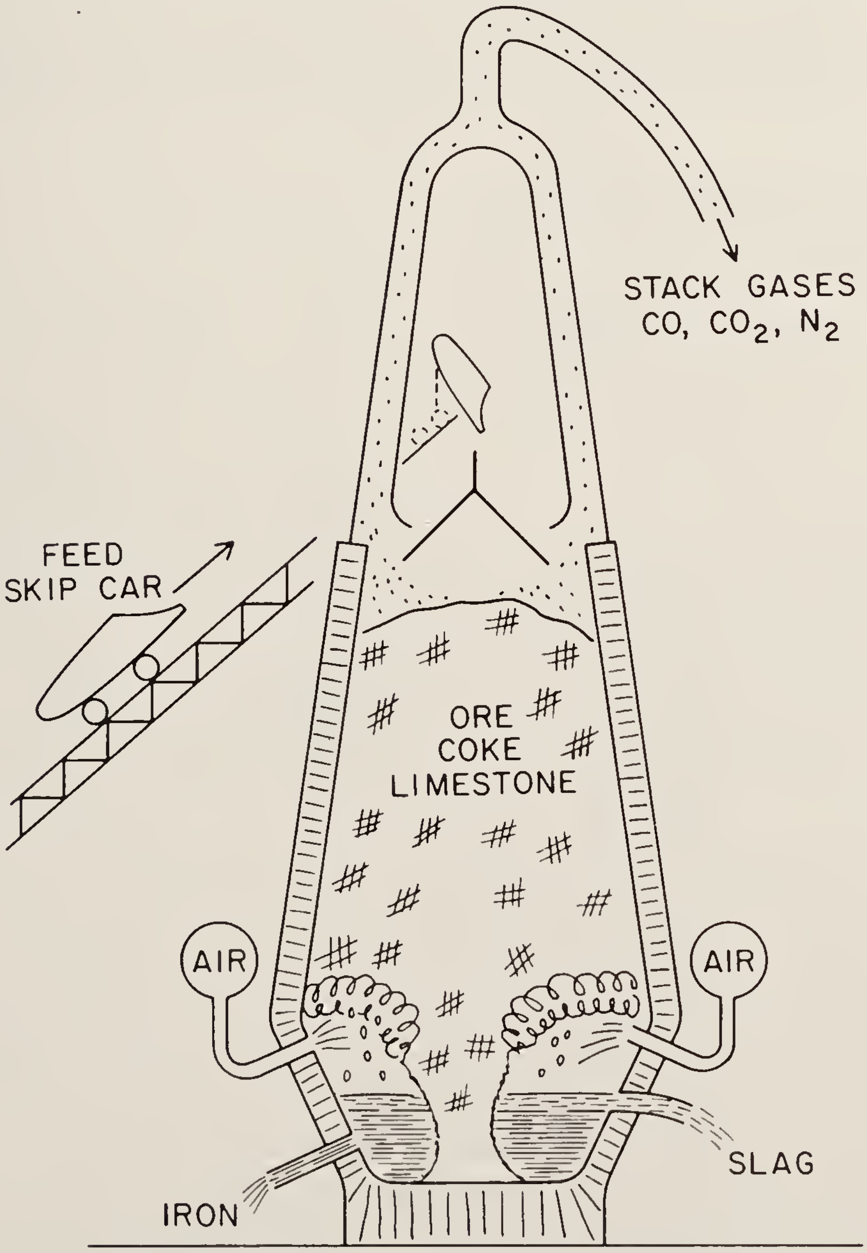


Fig 1 Configuration of typical blast furnace; 80 m high overall.

naces which have enabled them to compete successfully over the years are that they work by gravity, have a high throughput, and have no complicated machinery in the reaction zone. They conserve energy very well, and can be engineered to go on and on without interruption for several years. Actual chemical reactions take place in the center of the descending mass and away from the walls. All these advantages are improved by increased size, so that it is not surprising that their evolution has been in this direction.

The largest furnaces today are in Japan. A large furnace built recently by Bethlehem Steel in the United States may be taken as an example of modern furnaces. It has an inside hearth diameter of 13.6 m, and an interior working volume equivalent to 12 or so good sized houses. It can produce 8000 tonnes of iron a day! It is equipped with several hundred sensors for temperature, pressure, flow rate, etc., and is computer controlled. It cost $200 million to build in 1977. The steady operation of expensive equipment like this must be ensured, and so the quality and regularity of feed materials must be closely controlled. No longer can random sized lumps of ore be fed. Modern feedstock typically would be about 50% pellets of preconcentrated, well-sized ore and 50% sinter of ore and limestone. The object is to ensure a permeable bed of solids so that gas-solid chemical reactions can proceed efficiently. Coke must be of high quality, porous yet strong. The main cost incentive is to reduce the coke-rate, the number of kilograms of coke required to produce 1 tonne of liquid iron. In modern large furnaces this can be reduced to about 400 kg/tonne, with the help of about 75 kg/tonne of heavy oil or tar blown in with the air supply. Not only is the coke the single most expensive feed, but as it is essentially the sole source of the sulfur, keeping the coke-rate down reduces the sulfur problem. Table II is a comparison of old and new blast furnace technology.

Table II. Comparison of blast furnaces

	State of art in 1950	State of art in 1980		
		U.S. Steel No. 8	Bethlehem Steel "L"	Oita No. 2 Japan
Diameter (m)	9.5	9.8	13.6	15
Volume (m^3)	1275	2500	3700	5000
Tonnes/day	1470	4500	8000	12000
Tonnes/day/m^3	1.2	1.8	2.2	2.4
Coke rate kg/tonne	800	545	443	409

The smallest of the modern blast furnaces listed will produce about 1.6 million tonnes of hot metal a year and this, with scrap, will result in perhaps 2.5 million tonnes of steel. The present operations at SYSCO are in the 0.75 to 1 million tonnes/year range, and are provided by 2 relatively old furnaces which each produce about 800 tonnes/day. The coke rate can be 680/kg tonne, although this depends on the amount of limestone that must be added to take care of the sulfur. Thus the iron that they make is relatively expensive. The economy of size of 1 very large furnace is

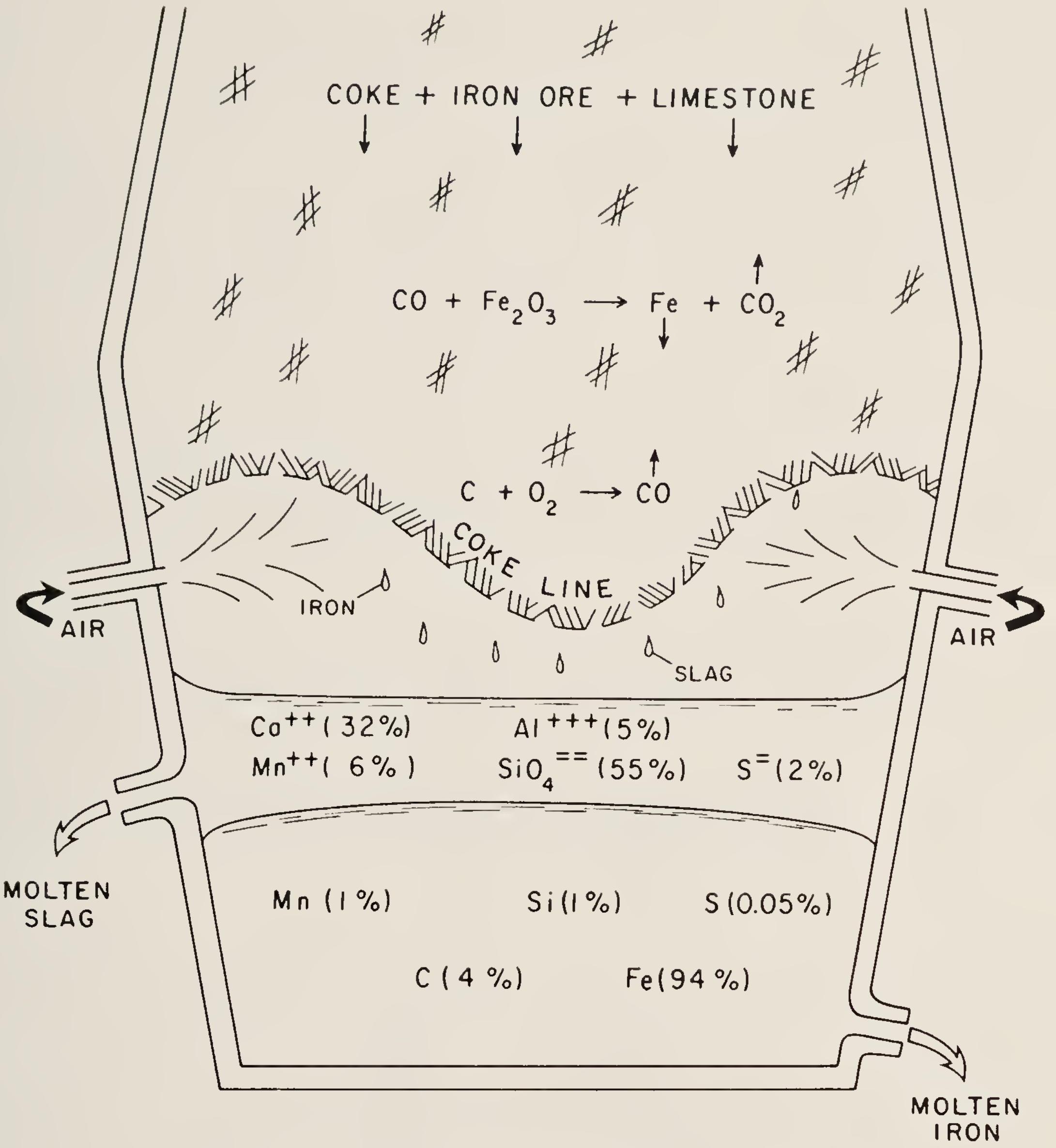


Fig 2 Chemistry of blast furnace.

just not applicable to the present SYSCO situation, although it would have been correct for the proposed CANSTEEL operation.

Before we leave the blast furnace, let us examine its chemistry in a simple manner (Fig 2). In the hearth of the blast furnace a metallic solution is in contact with an ionic solution, and is in more or less thermodynamic equilibrium with it and the gas phase, the latter setting the oxidation potential of the system at a very low level. The values given for the concentration of the various species (in weight percent) in the 2 solutions are merely typical of blast furnace operation. There has been much research over the years on all aspects of this equilibrium, and it continues today. For example, could we push this equilibrium in some desired direction by the judicious application of an EMF? The most troublesome impurity in the liquid iron is sulfur, and this comes almost entirely from the coke. Its elimination has been the subject of a study by AGRIM, as mentioned later.

Direct-Reduction

A mini-mill like SYSCO only requires a mini-iron plant. There are a variety of direct-reduction processes, either under development or actually operating which are of this scale. In general they give a solid iron product rather than a liquid, so that subsequent steel making processes have to melt as well as refine, and separation of impurities is not as good as in the blast furnace because there is no liquid slag to carry off the impurities.

A successful direct-reduction operation has been the MIDREX process, used by SIDBEC-DOSCO in Quebec. This is a solid-state reduction of pellets by means of reformed natural gas brought in from western Canada by pipeline.

The CO_2-product gas is used to partially oxidize (reform) the natural gas into CO and H_2, the heat of the reaction providing the necessary temperature for the reduction of the ore. Two units produce about 1.1 million tonnes per year of 93% iron, the main impurity now being oxygen rather than carbon (the latter 1%) as in blast furnace iron. The attractiveness of the MIDREX process (and others like it) is that the units do not have to be very large to obtain economies of operation, and 0.5 million tonnes per year is a feasible package. Their output compared with capital cost is good; a million-tonne per year plant has a volume productivity of 10.4 tonnes/day/meter^3 as compared to only about 1.7 for a comparably sized blast furnace. Of course these units do not make liquid iron so their output has to be melted later. The great thing about a blast furnace is that it is a combination gasifier, reducer, and melter.

When iron is made in the future at Sydney a direct reduction plant of the general MIDREX type would be sensible. However, the steel plant was located where it is largely because of coal, and its long-term viability may remain tied to this fact. Therefore, a direct reduction process which would utilize coal directly, or the reformed gases from the gasification of coal, would seem to be more appropriate. The STELCO-LURGI process is an example of the first.

There are many strategies available, but one that would allow the valuable coking properties of Cape Breton coal to be utilized would be to construct a large merchant coke plant, sell the coke abroad for use only in large efficient blast furnaces, and reform some of the coke-oven gas for local direct-reduction purposes. The developers of both the HyL and MIDREX processes have recently announced an extension of their processes to the reforming of coke-oven gas. The remainder of this strategy would be to pipeline excess coke-oven gas for other industrial or commercial uses, and refine the reduced iron pellets in an electric arc furnace powered by electricity generated by the combustion of lower grade coals.

As might be expected, a great deal of research has been performed on the fundamentals of the kinetics of direct reduction of iron-oxide by reducing gases. It proceeds by a stepwise reduction from Fe_2O_3 to Fe_3O_4 to FeO and finally to Fe. The main kinetic resistance is countercurrent diffusion of gases through the solid layers and is affected by the density of the pellet and impurities.

It should be pointed out that, in general, the efficiency of all these high throughput units depends upon efficiently bringing up the large quantities of raw materials. In this respect we may note that the best reductant is the electron itself, and that it can be moved simply and cheaply along wires. Therefore, there are hypothetical advantages to an electrochemical process for reducing iron oxide to iron. Here we are not suggesting the electroplating of iron from aqueous solution, but from the fused oxide itself. One problem is that these molten oxides exhibit electronic conductivity rather than ionic, and so it comes down to finding some additive which would produce a fused salt from which iron could be plated. This was the kind of technology that allowed the aluminum industry to be successful and might be a worthy subject for research for the iron industry.

Steelmaking

No matter how iron is made from iron oxide, there must be a further refining step to make steel. Liquid iron from the blast furnace contains about 4% carbon, and this must be removed along with the other impurities such as silicon, manganese, and sulfur. This is accomplished in a variety of batch processes, the chief characteristic being that the oxidation potential of the system is much higher than that in the blast furnace, so that the chemistry of the system is shifted towards much lower carbon contents than the 4% of the liquid iron. For example, 1% carbon steel is a high carbon steel, 0.8% is normal for rail steel, and mild steel around 0.1%. The important requirement for any steelmaking process is a good supply of oxygen. In the discussion to follow it may be noted that technological advances have been made by improving the rate at which oxidant can be supplied to the reaction interface between the oxidizing medium (be it gas or liquid slag) and the liquid iron.

Bessemer Converter vs Open Hearth Furnace

The era of quantity steel, as opposed to cast iron, began in about 1865 when Bessemer patented his process of blowing air through a bath of molten iron. It is fortuitous that iron itself will not oxidize until after carbon and silicon have been removed, and this is what makes the whole thing possible. Bessemer's process was closely followed by the development of the open hearth furnace, and for 50 years the industry saw these 2 processes make essentially all the world's steel. The basic differences in the 2 are worth pointing out as they have relevance today. Figure 3 shows that the metal bath in the open hearth is shallow but large in surface area, and is heated by an overhead flame, while in the Bessemer converter the metal is deep, of small area, and unheated. In the Bessemer process the air bubbled up through the molten iron and, giving a high specific rate of oxidation, resulted in a high production rate (about 100 tonnes steel/h). The capital cost for a given output

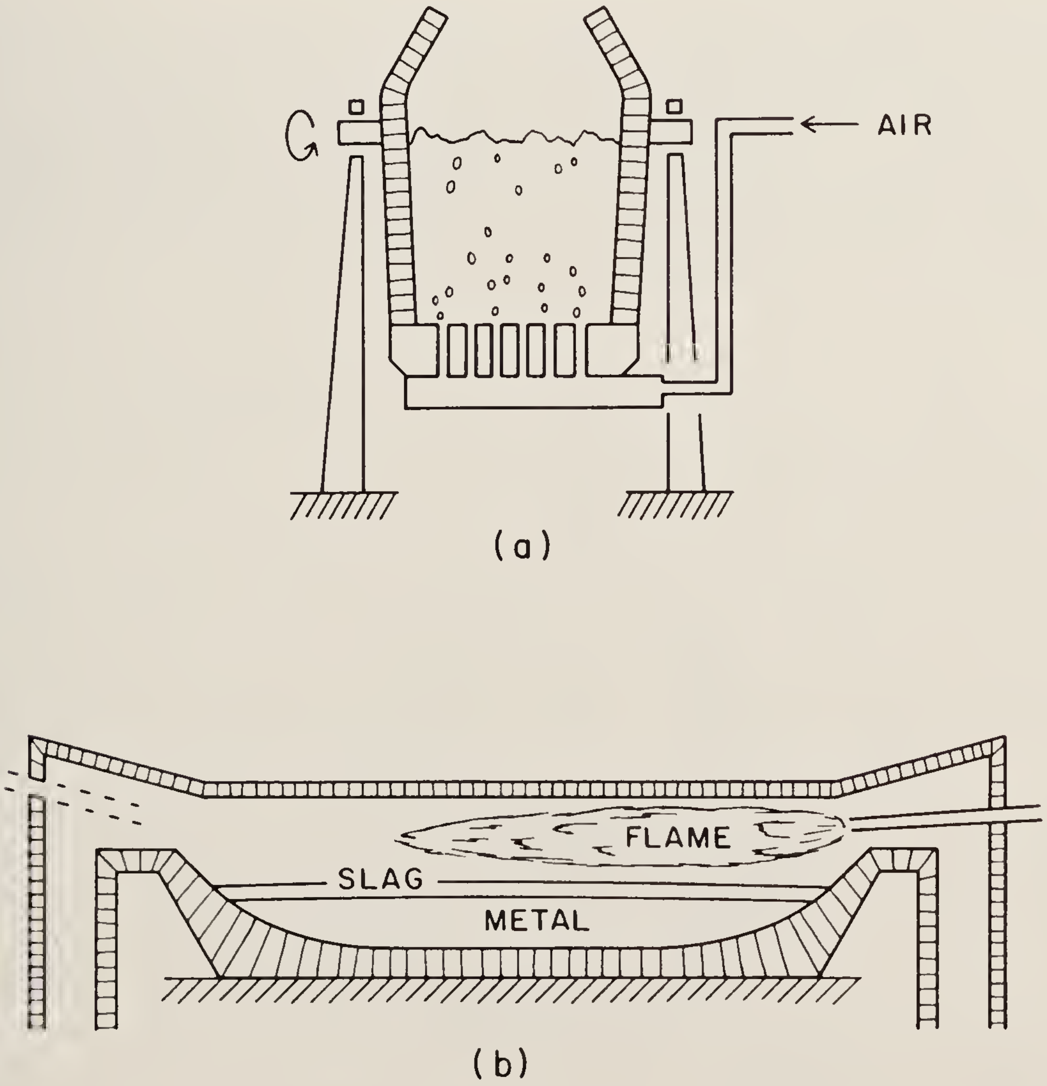


Fig 3 Comparison of configurations of Bessemer converter (a) and open-hearth furnace (b).

was low. However, the converter could not melt scrap, chemistry was not easily controlled, the range of impurities that could be handled was limited, and nitrogen dissolved in the steel. Another problem was the serious attack on the firebrick bottom by iron oxide, although to counter this the converter was made with an easily replaced bottom. The chief virtues of the open hearth furnace were large size, the ability to melt scrap, and controllability. Its disadvantages were that the oxidation rate was limited by the slow diffusion of oxygen (to give a production rate of about 20 tonnes/h), the capital cost was high, and repairs were costly.

The percentage of the world's steel made by the Bessemer process peaked in 1875 at about 80%, and slowly declined thereafter as the open hearth became more popular. The forerunner of the present SYSCO was built in the early 1900's, when the open hearth process was emerging as the dominant technology, and in its day it was a modern integrated facility. By 1950 the conventional OH furnace had reached its peak of use and was making 70% of the world's steel. Furnaces were large (ones of 600 tonnes are still used in USSR) and becoming quite sophisticated.

Electric Arc Furnace

The electric arc furnace began as a means for getting heat into a furnace without using an oxidizing flame; thus scrap could be better melted and as well the temperature and chemistry kept under better control. Vessels tend to be deep and of small surface area, so that oxygen enters the top by diffusion and the specific oxidation rate is low. However the arc furnace is usually used for making specialty steels such as stainless and high-carbon, or for melting pre-reduced pellets, so that there is less requirement for high rates of carbon removal.

Processes Using Gaseous Oxygen

It is interesting to note that the original patent of Bessemer included the possibility of blowing with pure oxygen as well as air. Of course in the late 1800's tonnage quantities of oxygen were not available so this prospect had to wait for a later time.

The war and post-war years saw first Germany, then the United States and USSR, develop tonnage oxygen plants for missile propulsion, and this finally allowed the

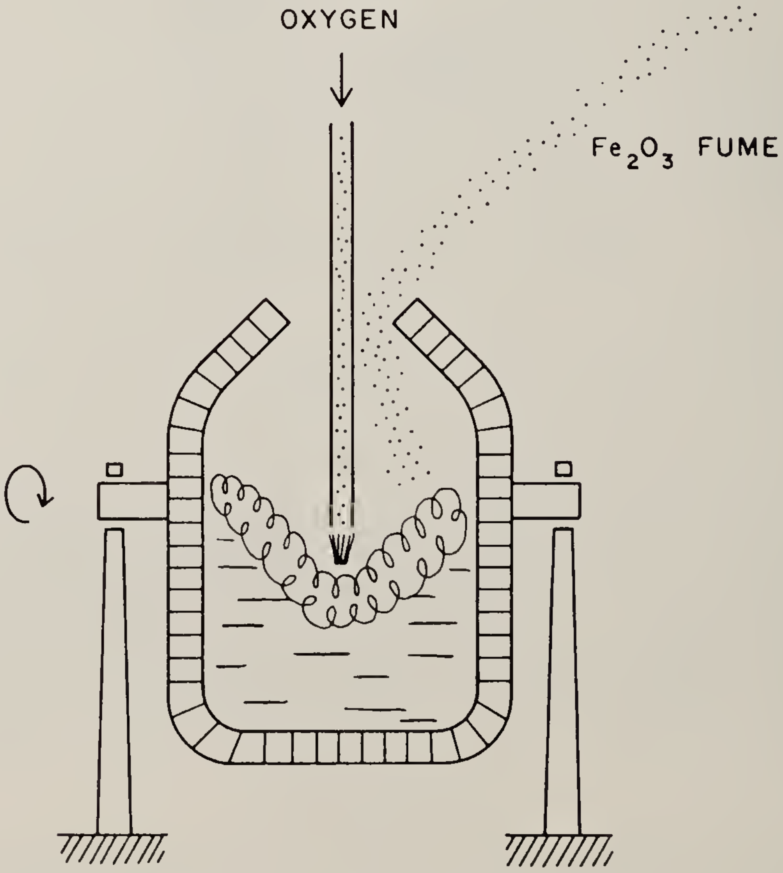


Fig 4 Configuration of basic oxygen process (BOP)

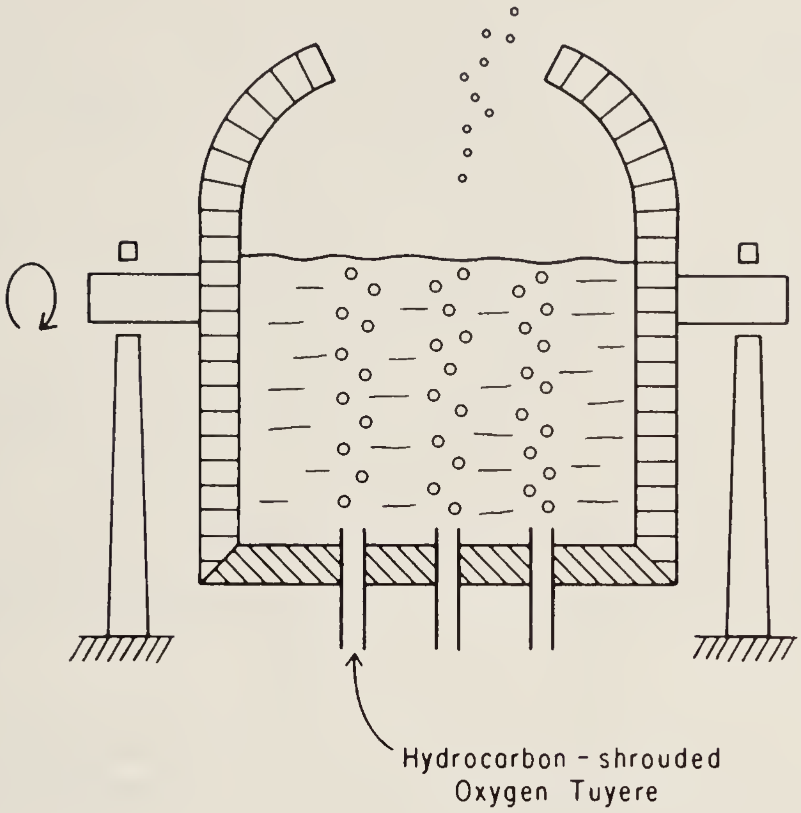


Fig 5 Configuration of Q-BOP.

promise inherent in Bessemer's original patent to be at least partly realized. It was in Austria that the LD process was developed and Figure 4 shows the configuration. Oxygen is blown down onto the surface of the metal at such a rate and pressure that a quite violent oxidation occurs, considered to take place mainly at the large reaction interface of an emulsified mixture of metal and slag. This process, which has become called simply the basic oxygen process (BOP) rapidly became popular and after 1970 overtook the OH process in the percentage of steel made. The speed of refining is the important feature. Specific blowing rates of $3m^3$ of O_2/minute/tonne can be achieved for large 200 tonne vessels. This means that 200 tonnes of 4% C. iron, containing 8 tonnes of carbon, can be refined in about 20 minutes. This is a reaction rate of 2.7×10^3 moles/second, and means that only about 100 of these vessels operating continuously could refine the world's steel production. They can melt up to about 25% scrap, and computer control of the blow maintains correct chemistry. A great deal of fine FE_2O_3 fume is evolved, and of the capital cost of a BOP about 20% has to be expended on controlling atmospheric emissions. It is interesting to note that DOFASCO in Hamilton was the first North American plant to install a BOP.

It was not long before OH furnaces were also equipped with top-blown oxygen lances, and this helped to bring refining times for a 300 tonne furnace down to 5-6 hours. This has prolonged the life of many an OH shop, including SYSCO's. The fume problem is severe because of the large bath area, and in general this configuration is not the ideal one for the top blowing of oxygen.

The most recent development of the BOP is the Q-BOP, where oxygen is injected through bottom tuyeres. This is the logical development of Bessemer's idea, although there is a crucial difference (Fig 5). One of the problems with the original Bessemer converter was the continuous attack of FeO on the bottom refractories and the burning back of the tuyeres. This problem potentially is worse for injection of pure oxygen, and the solution which allows the Q-BOP to function was to shroud

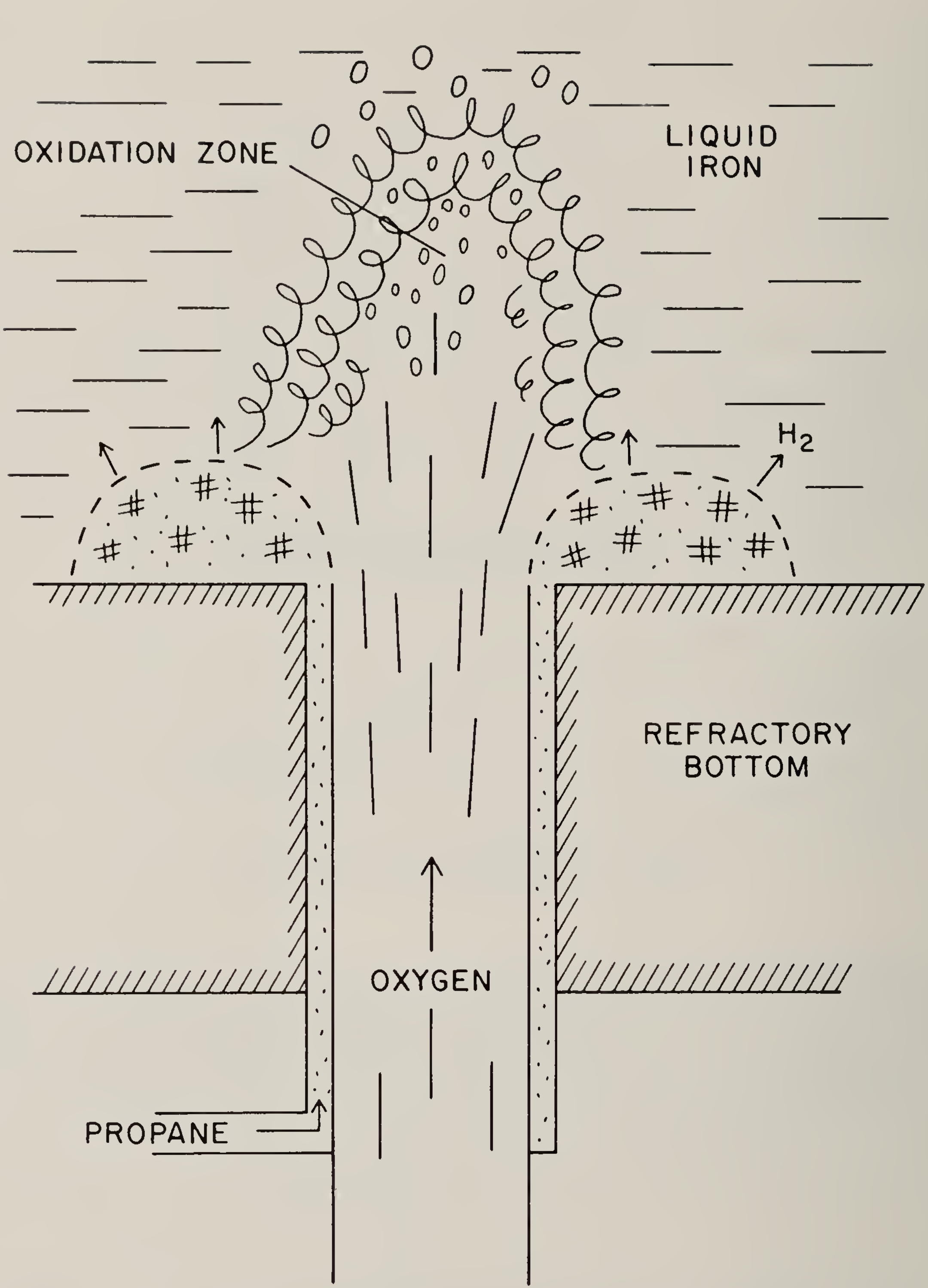


Fig 6 Operation of hydrocarbon-shrouded oxygen tuyere.

the oxygen pipe with an outer annulus through which a hydrocarbon gas (e.g. propane) is passed (Fig 6). The hydrocarbon cracks into hydrogen and carbon as it emerges from the annulus, and as this is an endothermic reaction it cools the end of the tuyere. A porous "mushroom" of iron-carbon is built up at the annulus and protects the pipe and the refractory, although this is still the weak part of the equipment (Parish & Pengelly 1979). One important advantage of Q-BOP over BOP is that there is less fume and less slopping of slag and metal. Blowing rates can be greater, and are beginning to get to the point where reaction rates will be limited by the chemical step at the gas metal interface, rather than by the rate at which oxidant can be brought up to the system. The Q-BOP process has an interesting history and Nova Scotia has a connection with it. Two Montreal engineers working for Canadian Liquid Air, G. Savard and R. Lee, invented the hydrocarbon shrouded tuyere in the 1950's, and some of their first, small-scale trials were carried out in the steel plant in Sydney. After some years the rights to this invention were sold to a German firm which developed it into a workable steelmaking process. U.S. Steel now has the North American rights, and it was they who called it Q-BOP, Q for "quiet, quick and quality".

It was mentioned that OH furnaces became equipped with top blown oxygen lances to speed up steelmaking, and in like fashion when the hydrocarbon-shrouded tuyere became available this also was adapted to the OH. SYSCO tried this several years ago in a process known as SIP, for Submerged Injection Process. Details of the process were not made public, but apparently there were several tuyeres per furnace, and the productivity was high. However, the experiment was discontinued, probably because of severe refractory wear and general unreliability. It should be noted that the bottom of a Q-BOP vessel is relatively small, has 10 or so tuyeres, and when too many tuyeres burn back or plug up, the entire bottom can be replaced in a reasonably short time. The OH furnace has a relatively large bottom which cannot be replaced easily, and presumably fewer tuyeres are used. The depth of metal in an OH is not great, and it is depth of metal that makes bottom injection so efficient.

Bottom injection of oxygen seems to be the technology that will become dominant, as discussed in a recent paper by Parish and Pengelly (1979). The SIP process shares some of the advantages of this technology, and it may make sense to convert existing OH furnaces to this process. However, it should be considered only as an interim solution, the final one being a properly configured Q-BOP installation.

Summary of Steelmaking Processes

It should be pointed out that oxygen processes require that a large quantity of carbon be oxidized. The exothermic heat of that reaction allows some scrap to be melted, and allows the melt to attain the high temperatures required for subsequent operations such as vacuum degassing and continuous casting. The Q-BOP or BOP are ideally suited for refining the huge output of modern blast furnaces. However, iron from a direct reduction plant such as a MIDREX plant contains much less carbon, and a different refining process would be used. At SIDBEC-DOSCO the refining step is carried out in a large electric arc furnace. This might have to be the solution for SYSCO for the long run, with low grade coal used to generate electrical power.

Figure 7 is a comparison of steelmaking methods from Bessemer's time, showing how processes have taken over from one another. It is apparent that the BOP process is destined to predominate, in either the top or bottom blown version. At the same time the electric arc process will continue to grow, and perhaps what we will see in the future is a hybrid process combining both bottom blowing of oxygen with assistance from electric arc or electric plasma. The advantage would be in the proportion of scrap that could be utilized; this is now down at about 20% for a Q-BOP.

However, it has been remarked (Callenfels 1979) that steelmaking, and indeed a whole range of capital intensive industries, is changing over from a period of

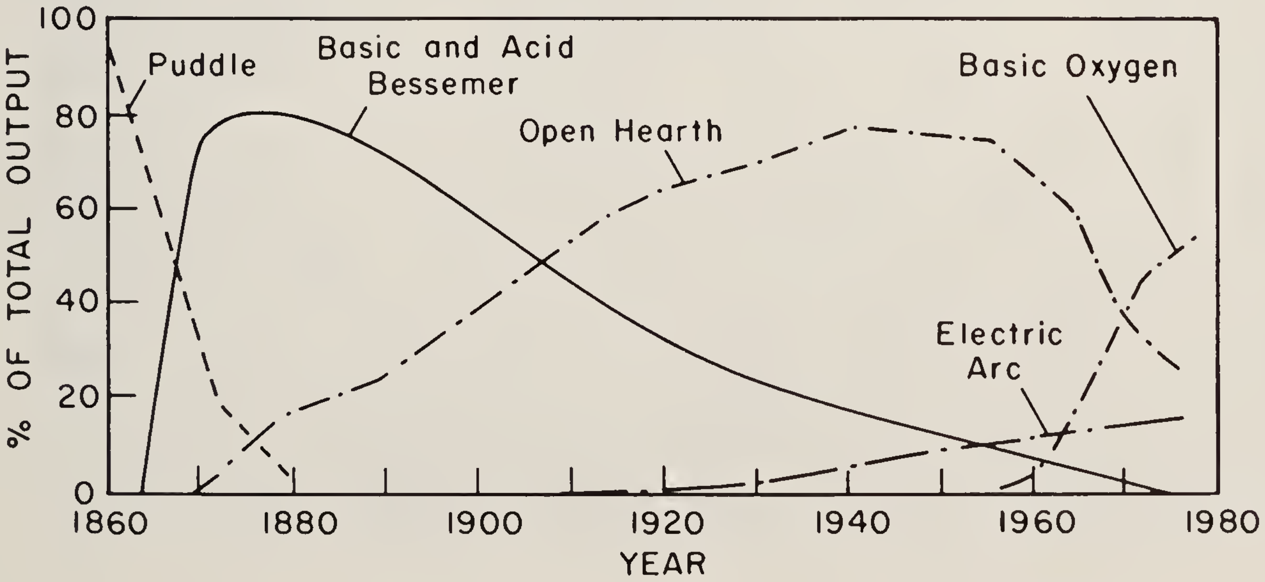


Fig 7 Development of some processes in the steel industry.

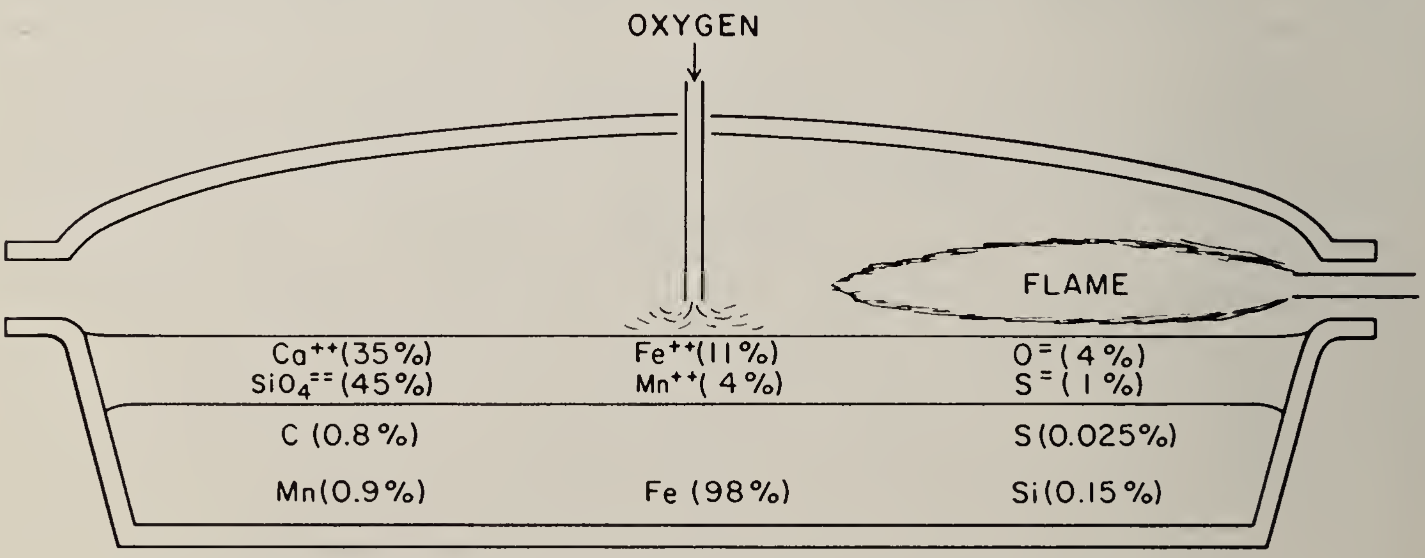
"technology push" to "market pull". In the past nearly every option that technology had to offer could be absorbed easily by a rapidly expanding market. Now we have the stagnation that is inherent in a mature economy, and it will be society as a whole that will determine the "market pull" and thus set the pattern and rate for technological innovation.

To finish this discussion of steelmaking it would be appropriate to illustrate its chemistry. Figure 8 gives some representative concentrations (in weight %) for an open hearth operation; other steelmaking processes would not be very much different. The important difference between blast furnace slag (Fig 2) and OH slag is that the latter contains free O^{--} ions, indicative of the high oxygen potential of the system, and that for the same reason the slag contains iron ions. This represents a potential loss of iron, so that when possible the OH slag is recycled back into the blast furnace. Slag chemistry is an important topic for research and will be mentioned later.

Some Research Problems in Nova Scotia

Industrial Research

We shall consider briefly two industrial-scale research programs. The first one was a cooperative program on the problem of sulfur in steel, financed by an NRCC grant to SYSCO under the Industrial Research Assistance Program scheme, and carried out by some members of AGRIM. The physical-metallurgical reasons why sulfur is deleterious in steel is a subject too large to pursue here, but it may be pointed out that sulfur rarely can be tolerated in concentrations over 0.05%, and for some sensitive grades of steel the maximum sulfur may be limited to 0.005%. Figure 9 shows MnS inclusions in a piece of reinforcing rod which had failed in a bend test. Figure 10 shows a scanning electron microscope image of particles of FeS_2 in coal; as mentioned previously the coal which is used to make coke is the source of the sulfur-in-steel problem. Figure 11 is an indication of how the sulfur partitions among the various phases of the overall steelmaking process; the numbers given are representative only, and will vary widely from steelplant to steelplant. Members of AGRIM investigated, among other things, methods of removing sulfur from coal, although that is not part of this discussion. SYSCO worked on means of removing sulfur from the liquid iron as it is in transit between the blast furnace and the open hearth. This was not really research or innovation, but was an effort to acquire the state of the



THESE FURNACES HOLD SEVERAL HUNDRED TONS OF LIQUID STEEL

Fig 8 Chemistry of the open-hearth furnace. Steel shown is typical of rail steel.

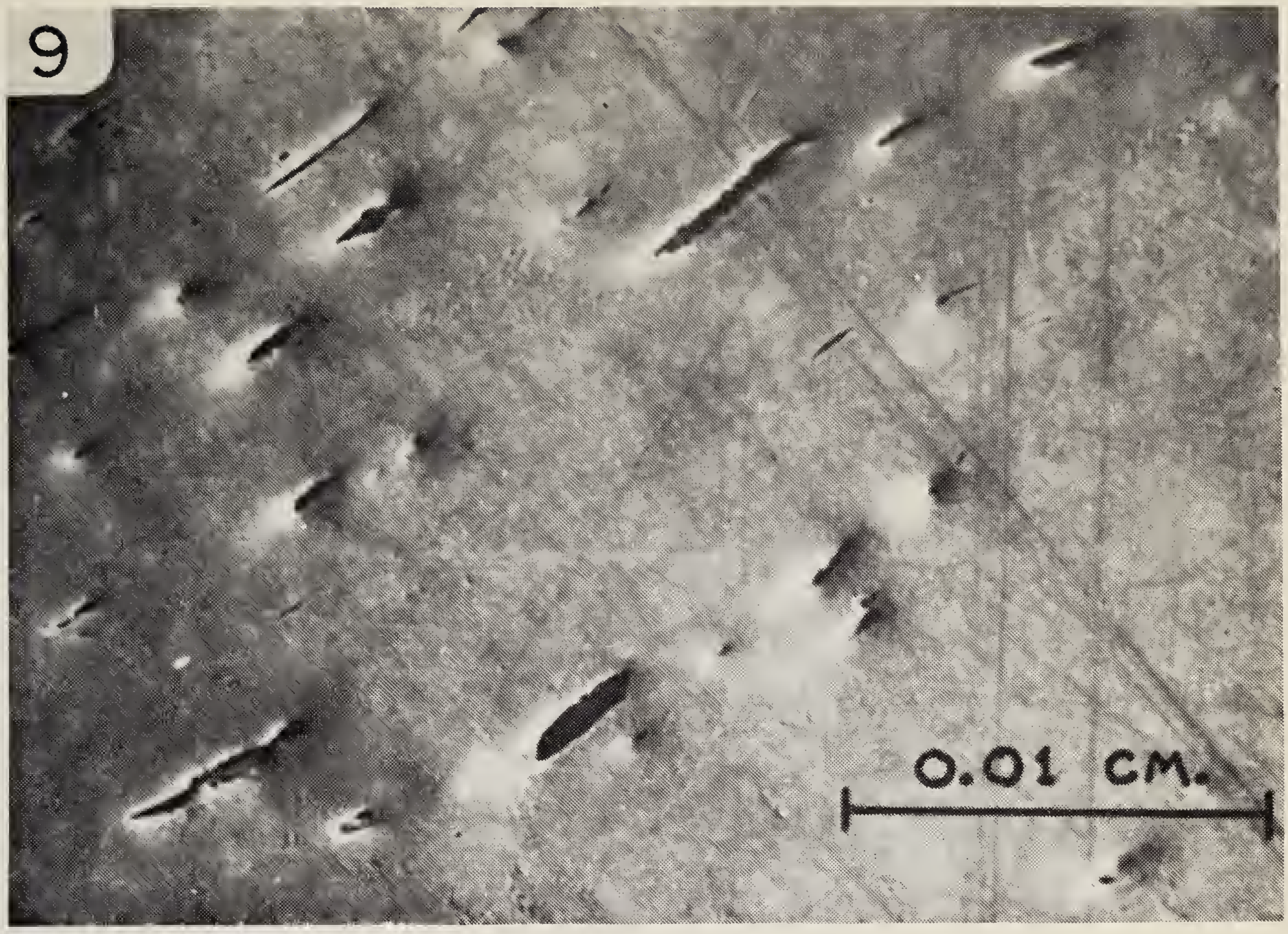


Fig 9 Manganese sulfide inclusions in steel.

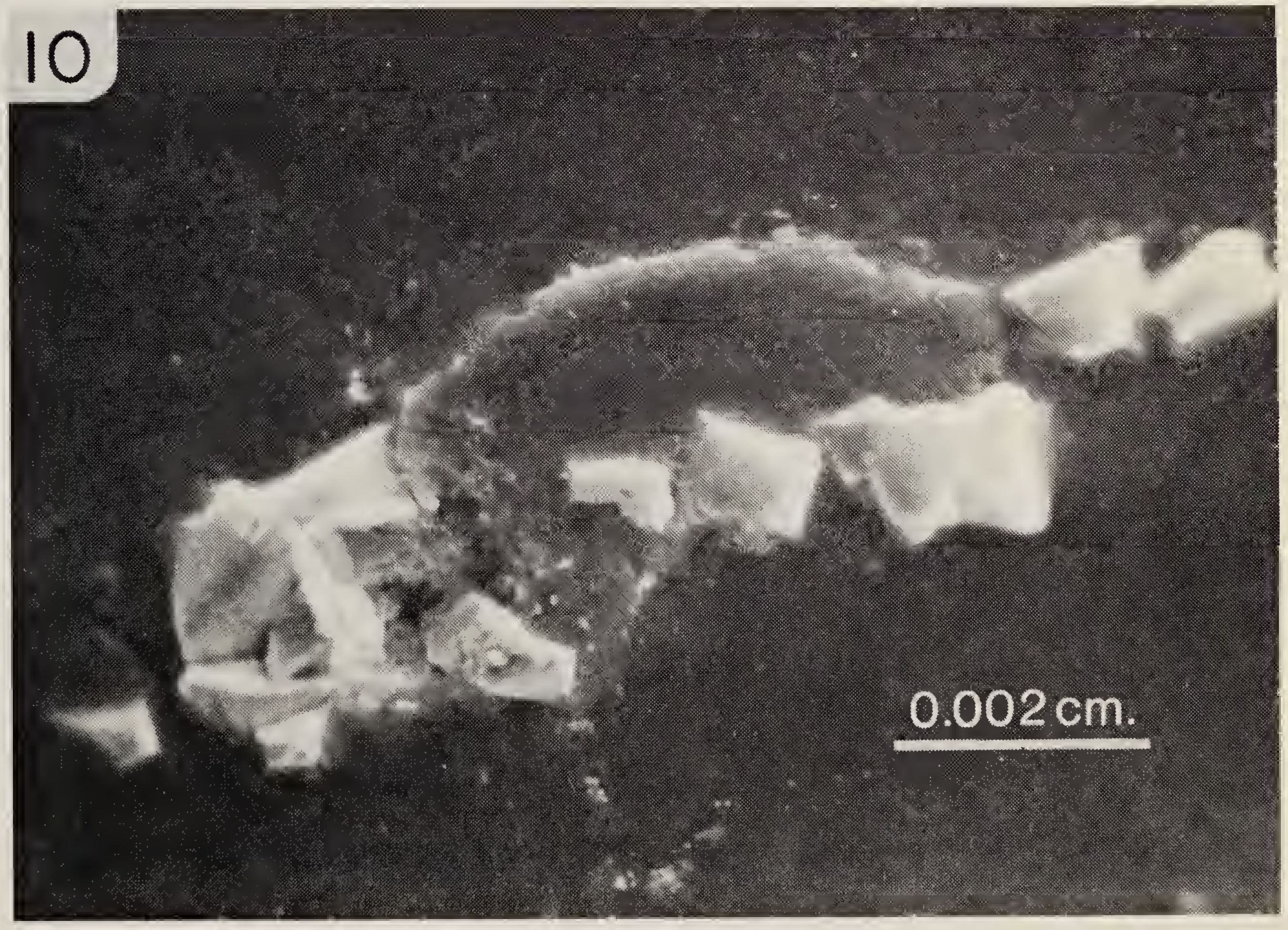


Fig 10 Iron sulfide (FeS_2) particles in coal from the Prince Mine, Cape Breton.

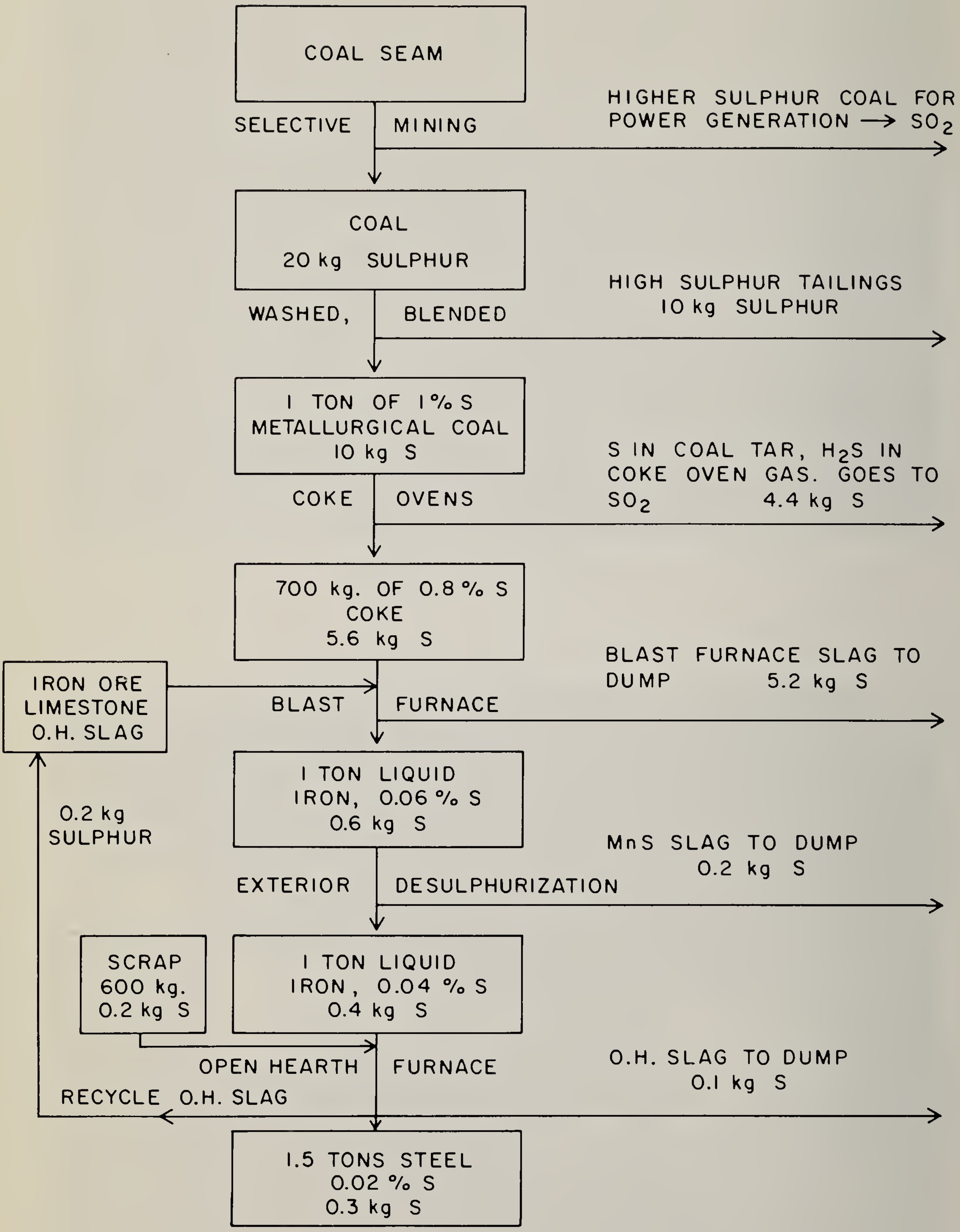


Fig 11 Sulfur pathways in steelmaking (ton = tonne).

art. In this case the final decision was to use "Magcoke", porous coke impregnated with magnesium metal. When a container of it is plunged beneath the surface of the liquid iron it causes a reaction between sulfur and vaporizing magnesium to give an MgS slag which can then be skimmed off the surface. Another part of the project was adding rare earth metals (such as lanthanum) to the steel as it is tapped; instead of long stringy inclusions of MnS (Fig 9), globular inclusions of mixed oxysulfides are obtained, and these are not so deleterious. This last work was a joint project of SYSCO and the Technical University of Nova Scotia.

A second piece of industrial research is on the problem of hydrogen in steel, the subject of a contract between the Atlantic Research Laboratory (NRCC) and SYSCO. Hydrogen dissolves in liquid steel as the atom (largely derived from the dissociation of water vapor) to a maximum of about 20 ppm. Its solubility decreases as the steel is cooled, particularly after the gamma to alpha transition. Hydrogen diffuses to grain boundaries, inclusions, and other nucleating centers, comes out of solution, and reforms to yield molecular H_2. The pressure of hydrogen that may be generated in such microvoids can become very large, hundreds of atmospheres. In some cases the strength of the steel is exceeded, and shattercracks are formed. These can be serious if not detected in the finished products, such as the rails which are SYSCO's main products. The present method of avoiding shattercracks is to take the hot rails as they are rolled and put them into insulated tanks, giving them the proper combination of time and temperature to allow atomic hydrogen to diffuse out to a safe 3 ppm. Hydrogen, being small, diffuses readily.

The present contract is on various aspects of the possibility of allowing unfinished steel, at the bloom size of 10" x 16", to soak in tanks. Experiments include work on the effusion of H_2 from cooling rails and blooms, such as the actual detection of hydrogen by gas chromotography, and computer simulations on the buildup of molecular hydrogen within steel sections of various sizes. One interesting series of experiments being done by R. Hay of Ecole Polytechnique employes "acoustic emission". The technique is a means of monitoring the formation of shattercracks by "listening" for them with acoustic transducers. Sound signals registered because of energy release upon formation of cracks within the bloom are fed to a microprocessor where they are analyzed for energy levels and position of origin within the bloom. Preliminary results indicated that high energy acoustic events correlate well with the formation of shattercracks. Acoustic emission may be a useful tool for determing in a non-destructive manner whether a particular bloom-cooling technique reduces the shattercracking phenomenon.

Fundamental Reseach

On a more fundamental laboratory level, it may be noted that steelmaking involves two quite different types of chemical solution: (1) a metallic solution with liquid iron as the solvent and containing solutes such as C, O, H, Si, Mn; (2) ionic slags containing cations such as Ca^{+2}, Mg^{+2}, Fe^{+2} and anions such as O^{-2}, SiO_4^{-4}, S^{-2}. These solutions are immiscible and the equilibrium between them, and the kinetics of exchange between them and the gas phase, are fruitful subjects for research.

The basic chemistry of the oxidation of solutes from liquid iron, especially carbon, is the essence of steelmaking. Figure 12 is a representation of the likely steps in the gaseous oxidation of carbon from iron (Hayer & Whiteway 1973). (A somewhat similar scheme, but one which includes charge transfer steps, may be envisaged when the oxidant is the O^{-2}, FE^{+3} of a slag.) We begin with oxygen in the bulk of the gas phase, and carbon in the liquid. Oxygen begins to flow to the metal surface but has to diffuse through an inevitable stagnant gas layer next to the metal. This

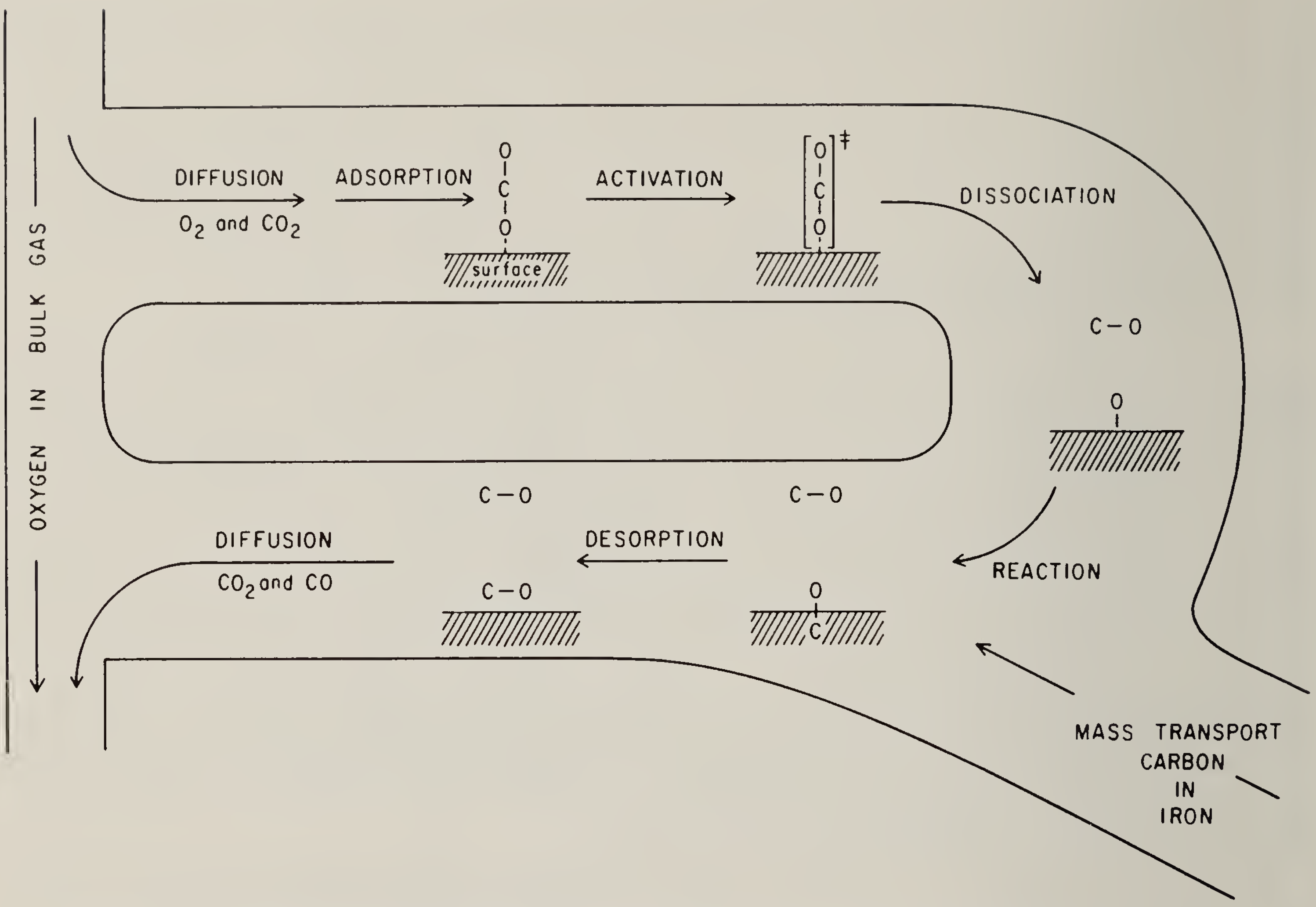


Fig 12 Steps in the oxidation of carbon from iron, using gaseous oxygen.

layer may be thick or thin, depending upon gas-flow factors such as turbulence. In the diffusion layer the oxygen reacts with the product of oxidation, CO, which is diffusing out in a countercurrent fashion. The oxidant now is CO_2, which continues to diffuse to the metal. This oxidant is adsorbed on a free surface site on the liquid iron, activated, and dissociated into a CO portion which desorbs, and an O portion which remains. This O reacts with a carbon atom diffusing up from the bulk of the molten iron to form adsorbed CO which finally desorbs and is carried out of the system. As the CO diffuses in the stagnant gas layer, it reacts with incoming oxygen as mentioned, and continues diffusing out as CO_2. Thus CO_2 is both the product and the reactant.

Each of the above steps contributes some kinetic resistance to the overall rate. However, at steelmaking temperatures of around 1600°, the intrinsic rate of reaction between adsorbed oxygen and carbon is very high, and seldom is rate determining. Figure 13 shows some data for the intrinsic rate, as well as an example of a typical laboratory experiment in which the actual rate fell well below this (Hayer & Whiteway 1973). Thus it is commonplace to find that it is the rate at which the oxidant can be delivered, through the stagnant gas layer next to the metal, that is rate determining. That is why the evolution of steel-making processes has been in the direction of maximizing the flow of oxygen to the metal.

Figure 14 is our concept (Whiteway et al. 1975) of the relationship among CO_2, CO and O_2 in the stagnant gas layer, assuming thermodynamic equilibrium. We have used a stabilized-zirconia EMF cell to probe down into the gas phase over oxidizing carbon, and have shown that this picture is largely correct. However, very near the

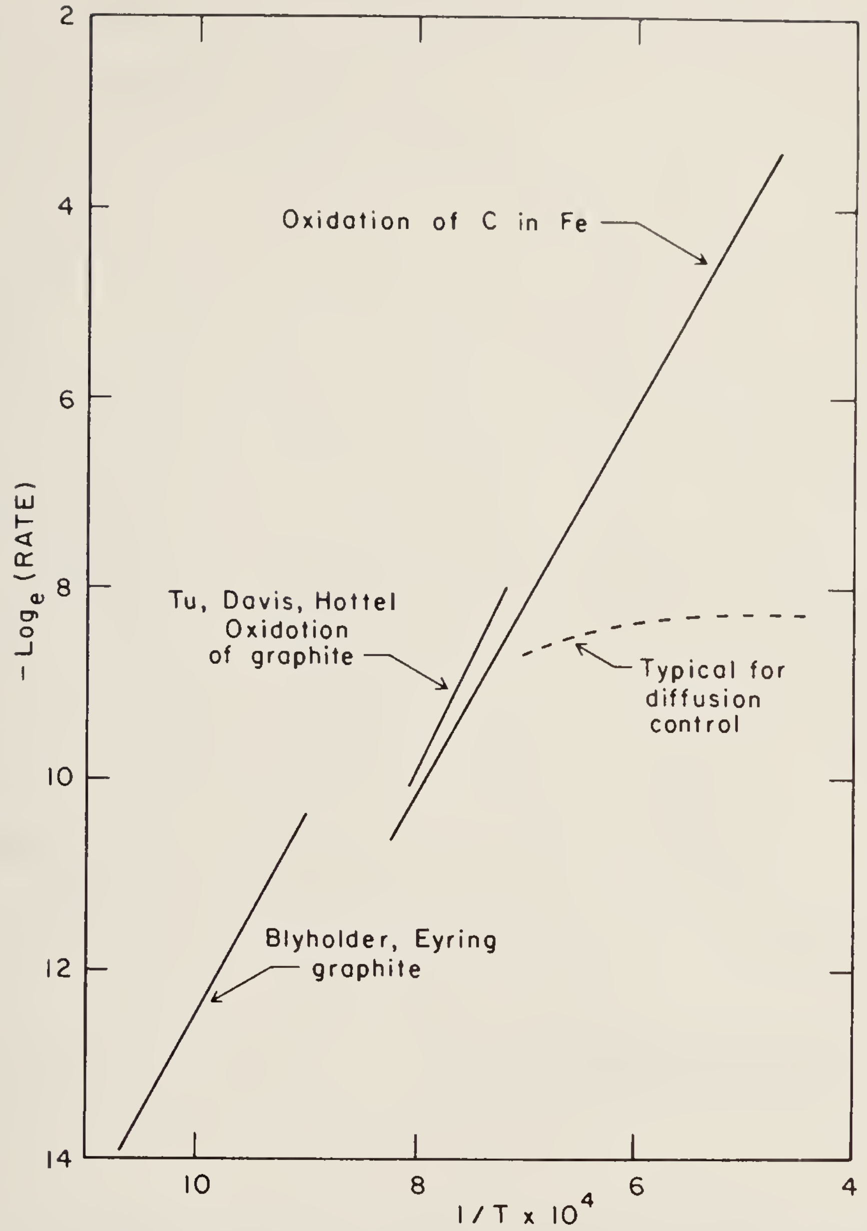


Fig 13 Intrinsic rate for oxidation of carbon by gaseous oxygen, including pure graphite and carbon dissolved in liquid iron.

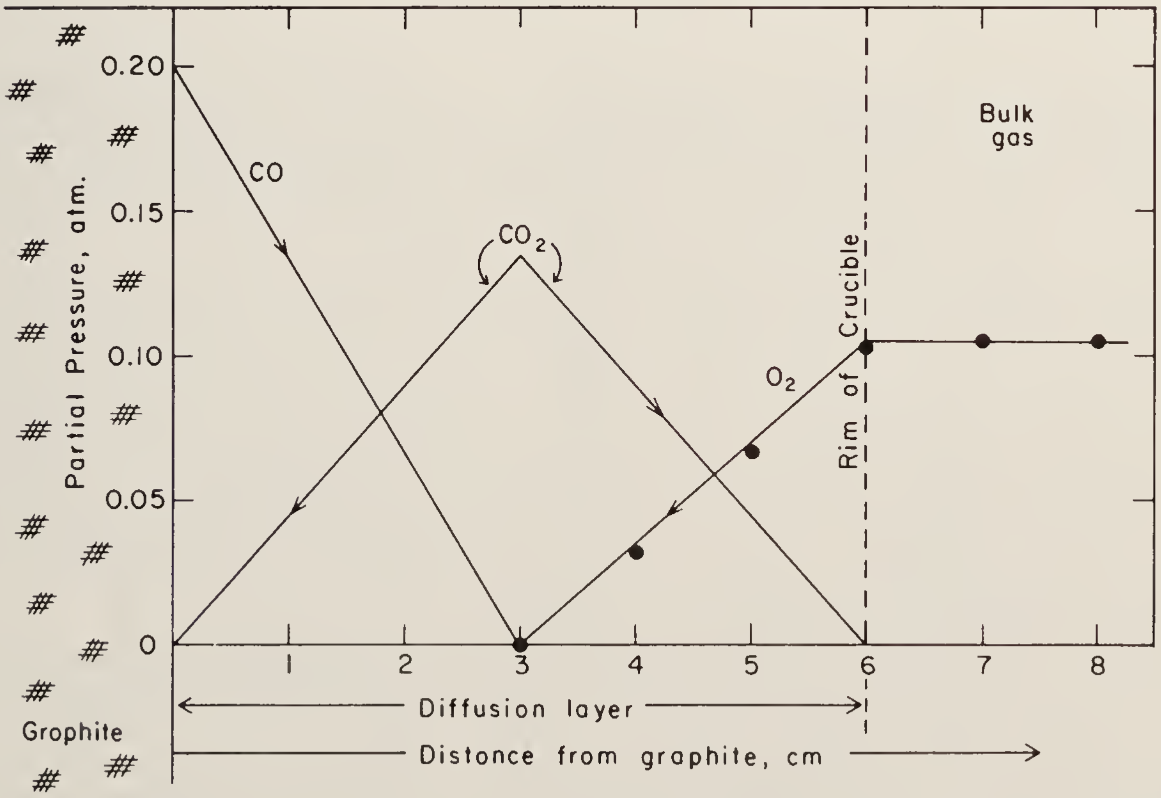


Fig 14 Relation of the species in the gas phase over oxidizing graphite.

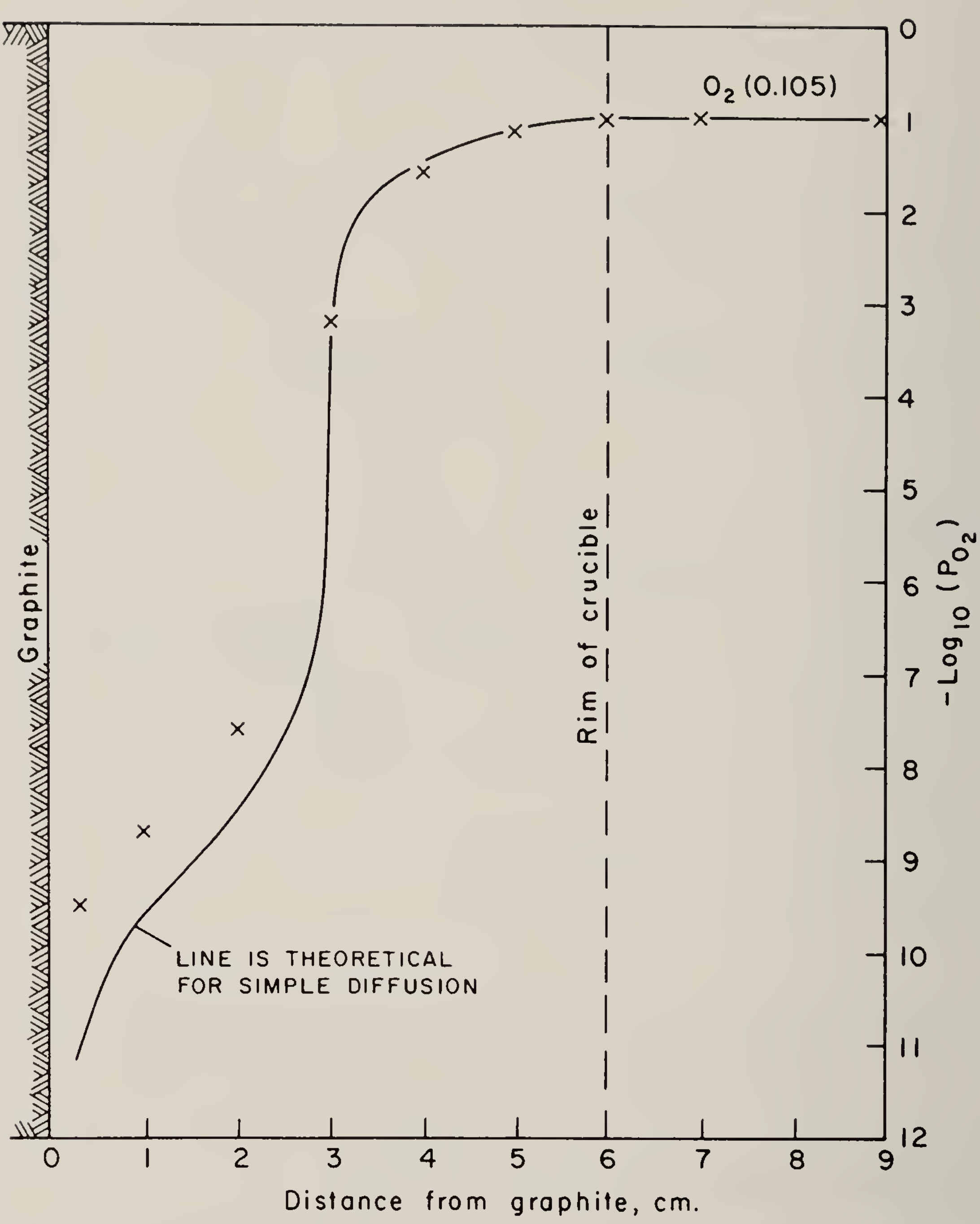


Fig 15 Experimental oxygen potential in the gas phase over oxidizing graphite.

graphite (Fig 15) the observed partial pressures of O_2 (of the order of 10^{-9} atmos.) are higher than that calculated from equilibrium conditions, indicating that some O_2 is escaping reaction with CO, and presumably this oxygen can react directly with the surface. If this is true under mild laboratory conditions it must be even more true when pure O_2 is lanced down onto a liquid iron surface.

Sulfur, when dissolved in liquid iron, is surface active. Therefore, there is some reason to expect that it could occupy surface sites and so render them unavailable for other reacting species such as CO_2. This was our (Hayer & Whiteway 1973) explanation for the experimental finding that while sulfur itself was not oxidized it slowed down the rate of oxidation of carbon (Fig 16). The behavior could be modelled by a scheme which took into account the competition for sites between CO_2 and S. These experiments are typical of many we have done on the kinetics of reaction of gases with solutes dissolved in liquid iron.

Turning to the investigation of the chemical nature of slags, I point out the great amount of work carried out at ARL by C.R. Masson and associates. Realizing the importance of the concept that slags are ionic, and that the silicate monomer SiO_4^{-4} tends to polymerize, Masson (1973) went on to develop models for the constitution of basic slags. The industrial importance of the concept of polymerization

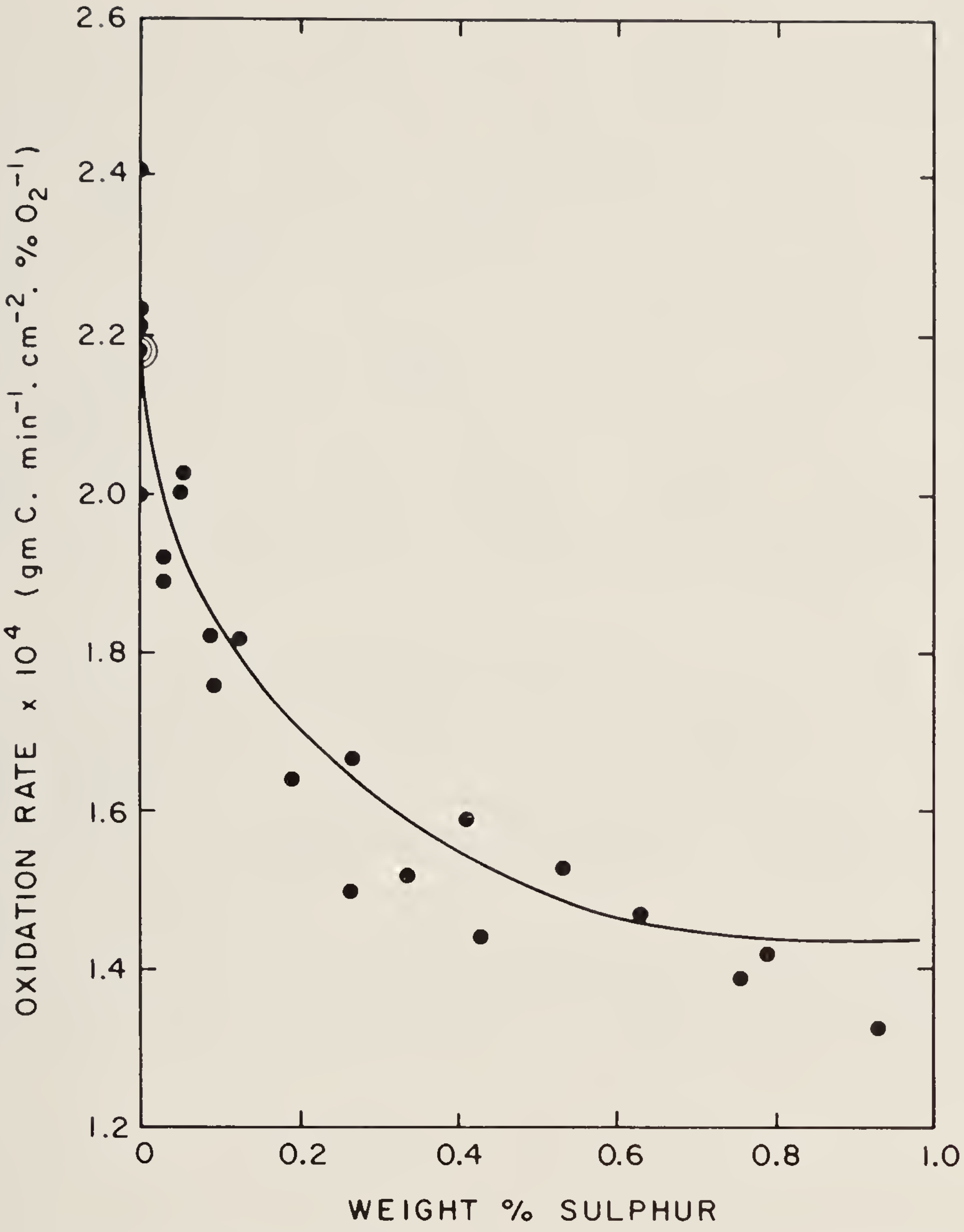


Fig 16 Effect of sulfur on the oxidation rate of carbon from liquid iron.

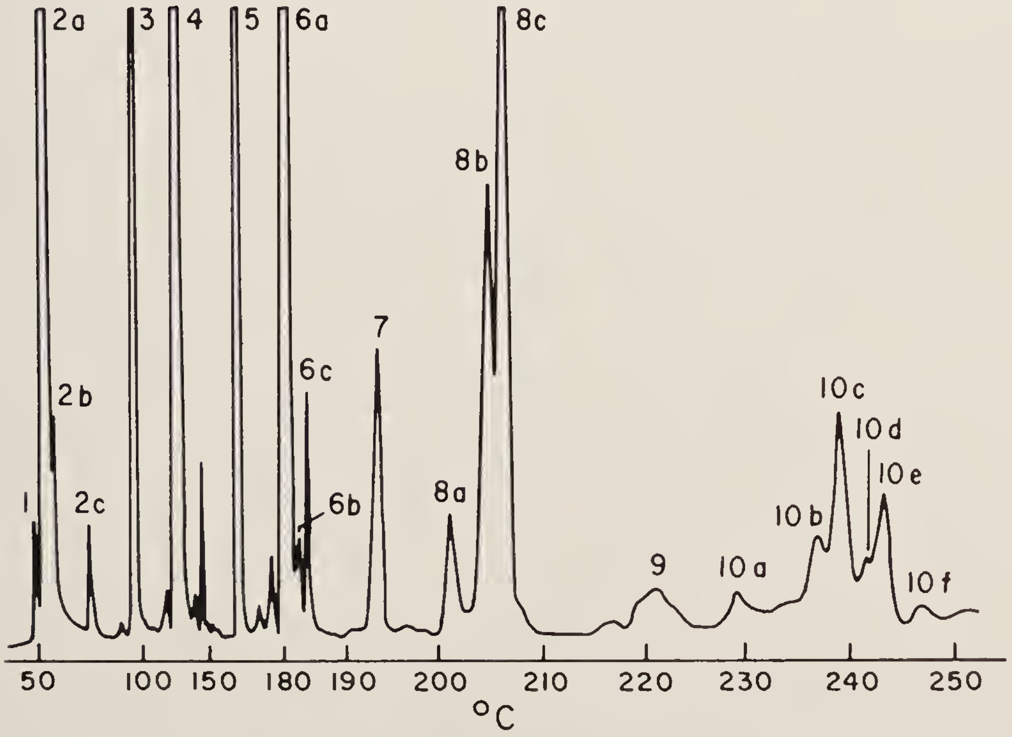


Fig 17 Typical chromatogram for open-hearth slag. The parent ions corresponding to some of the peaks are: 2a = O^{-2}; 4 = SiO_4^{-4}; 6a = $Si_2O_7^{-6}$; 8c = $Si_3O_{10}^{-8}$.

lies in its connection with the concentration of free O^{-2}, which is a measure of the oxidation potential of a slag, and its connection with the viscosity of slags. Masson and his co-workers (Masson et al. 1974; Calhoun & Masson, 1980) have also worked on the problem of detecting experimentally these ionic polymers, using a combination of gas chromatography and high-resolution mass spectrometry. Figure 17 shows species that occur in OH slags; these are gas chromatographic peaks, and include such identified species as Si_2O_6F (5-), Si_4O_{12}(8-), Si_4O_{12}(9-).

The viscosity of slags is an important industrial parameter, as a very viscous slag can increase refining times. We have developed (Caley et al. 1977) a rotating spindle viscometer which determines viscosity by measuring the torque on a rotated ceramic spindle. One application was to examine the relative fluxing powers of fluorspar (the usual flux added to reduce the viscosity of OH slags), ilmenite (a titanium ore), and strontium oxide. Figure 18 shows that SrO is a relatively poor flux.

Conclusion

I have attempted to give a picture of the present state of the art in steelmaking, the directions it may take, where Nova Scotia is now, and how Nova Scotia might move. It has to be admitted that the directions available to Nova Scotia are dictated by political, rather than technological, considerations. In addition I have given a few examples of industrial scale research and development being conducted in Nova Scotia, as well as some relevant laboratory-scale experiments. Many people have been involved in the research work quoted, and although not cited specifically, their contribution must be acknowledged. My exposure to the steel industry has been made possible by many friends at SYSCO, to whom I owe thanks; they labor at their craft in arduous circumstances.

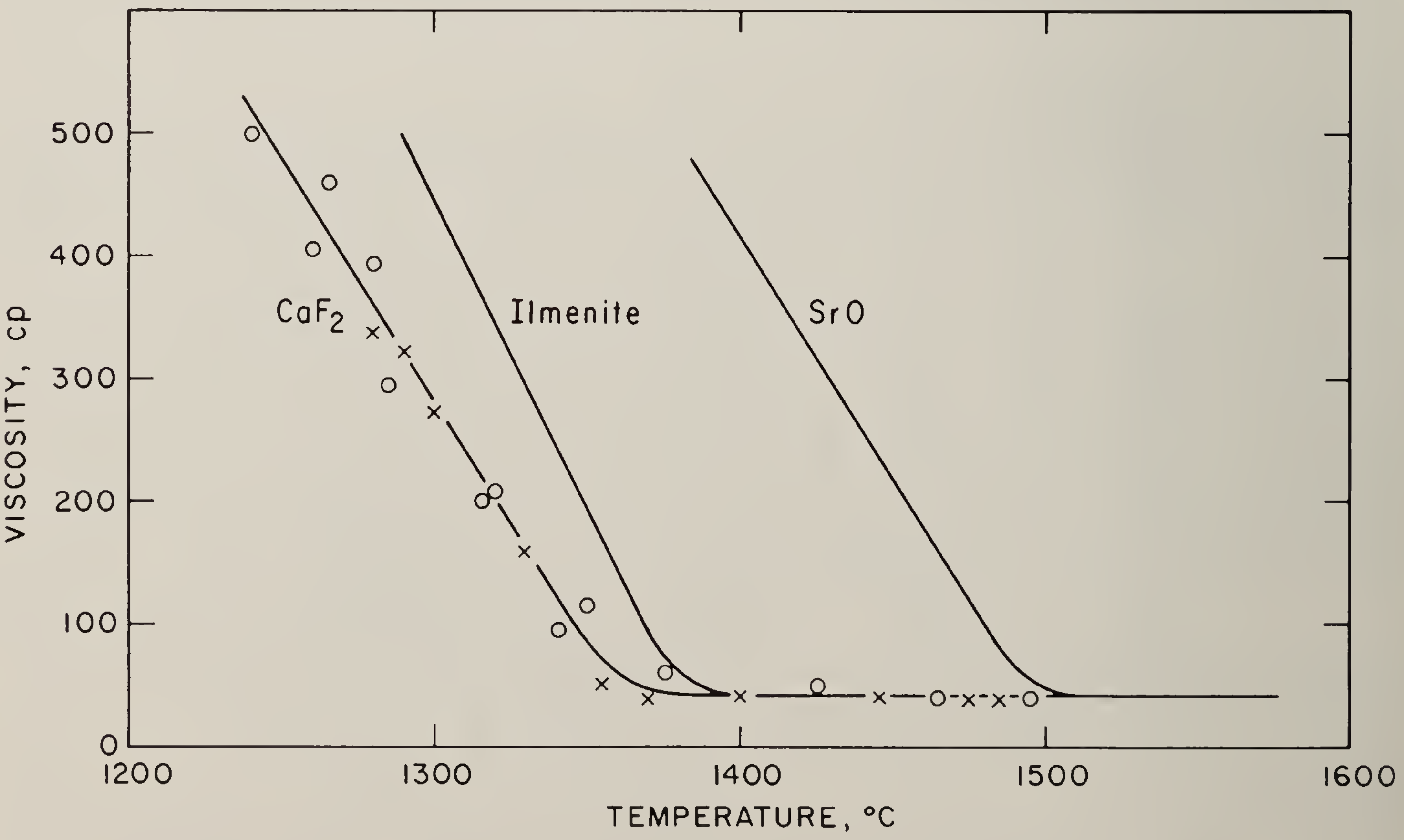


Fig 18 Viscosities of open-hearth type slags with various additives.

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Manuscripts should be typewritten, double-spaced on white paper 21.5 by 28 cm (8.5 by 11 in) with margins of 4 cm (1 5 in) Underline only material to be set in italics, and use capital letters only when letter or words should appear in capitals in the printed paper. Layout and style should follow that used in this volume The original copy and one duplicate are required. Each page of the manuscript should be numbered, the first page carrying only the title, authors' names and affiliations, and any necessary footnotes

Spelling should follow that of **Webster's Third New International Dictionary**, and authors are responsible for consistency in spelling

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Corrigenda

Volume 29 (1979) p. 128:

The reference to A.H. MacKay should read

MacKay, A.H. 1908. Fungi of Nova Scotia: A provisional list. *Proc. Trans. N.S. Inst. Sci.* 11: 122-143.

MacKay, 1913. A.H. Fungi of Nova Scotia: First supplementary list. *Proc. Trans. N.S. Inst. Sci.* 12: 119-138.

Volume 29(1979) pp. 483,488:

Sentence 2 of the Introduction p. 483 should read

Similar studies have been conducted on arctic breeding grounds in North America (Holmes & Pitelka 1968) and on over-wintering areas (Ashmole 1970; Baker & Baker 1973).

and to the References p. 488 should be added

Ashmole, M.J. 1970. Feeding of western and semipalmated sandpipers in Peruvian winter quarters. *Auk* 87: 131-135.

VOLUME 30 — Pagination

Owing to an unfortunate error, Part 2 of Volume 30 was paginated from page 1 instead of starting on page 117. To avoid further confusion, pagination in Part 3/4 runs on from Part 2. Accordingly, citations of articles in this Volume should indicate the part in parentheses after the volume number e.g. 30(2): 65-77.

PROC. N.S. INST. SCI. (1980)
Volume 30, pp. 89-100

EPIZOITES ON CANCER IRRORATUS SAY FROM THE GULF OF ST. LAWRENCE

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Abundance and distribution of invertebrate macroepizoites on the rock crab *Cancer irroratus* Say from Northumberland Strait in the Southern Gulf of St. Lawrence are described.

A convenient 3-digit code was devised for recording 66 surface locations on the crabs. Ten categories of epizoites were defined and then counted on 6,145 *C. irroratus*. Only 5 species had previously been reported on this crab. Ectoprocts, hydroids, bivalves and tunicates were frequent, whereas spirorbids, barnacles, gastropods, amphipods, anemones and limpets were less so.

Fifty-three taxa were identified on a subsample of 7 crabs. Ectoprocts, coelenterates and polychaetes had the highest species diversity. Their microdistribution upon the crab shell was influenced by the occurrence of setae on the shell. Patches of setae influenced the microdistribution of epizoites by accumulating detritus and providing a substrate suitable for small motile species like polychaetes and mites, while inhibiting the growth of some sessile forms such as barnacles, hydroids and ectroprocts. The blue mussel *Mytilus edulis* and the ectoproct *Alcyonidium polyoum* were the only deleterious epizoites noted. Although more female (76%) than male (58%) crabs were host to 1 or more epizoite categories, individual males supported as many as 6 kinds of epizoites, whereas the maximum for females was 3.

The number of epizoites on the crab was largely determined by the moult stage of the host, and seasonal abundance patterns of the 4 dominant epizoite groups reflected the moulting periods of the host. Males grew larger than females, and larger crabs of both sexes supported more kinds of epizoites than did smaller crabs.

Introduction

The purpose of the present study was to identify the epizoites of *Cancer irroratus*, describe their microdistribution upon the shell, and determine the seasonal incidence of the 10 most common kinds of epizoites. The crabs were from the Northumberland Strait in the southern Gulf of St. Lawrence.

Crustacean shells support fouling organisms such as ectoprocts, barnacles, bivalves and tunicates (DeTurk 1940; Dexter 1955). Invertebrate epizoites have been used as indicators of moulting (Van Engel 1958; Butler 1961; Terretta 1973; Haefner 1976) since newly moulted animals are uncontaminated and become more colonized through the intermoult period. *Cancer irroratus*, because of its relatively large size, hard exoskeleton, and its accessible, current-generating branchial chamber (Pearse 1947), supports a diverse epifauna.

Terretta (1973) found only 5 species in branchial chambers and on the exterior of over 1800 *Cancer irroratus*, and Haefner (1976) also reported 5 in a similar study of 254 *C. irroratus*. Apart from Heath (1976), who described the distribution of *Balanus crenatus* on *Carcinus maenas* and *Cancer pagurus* in Wales, there have been no quantitative studies on the composition and comparative distribution of epibionts upon the exoskeleton of *Cancer* species.

Methods

A total of 6,145 *C. irroratus* were captured, mostly from May to October 1975, in lobster traps set at 9 stations in Northumberland Strait near St. Edouard-de-Kent, New Brunswick (Fig 1). Depth and bottom type were verified at the start of each sampling period using depth sounder and bottom grab (Stasko et al. 1977).

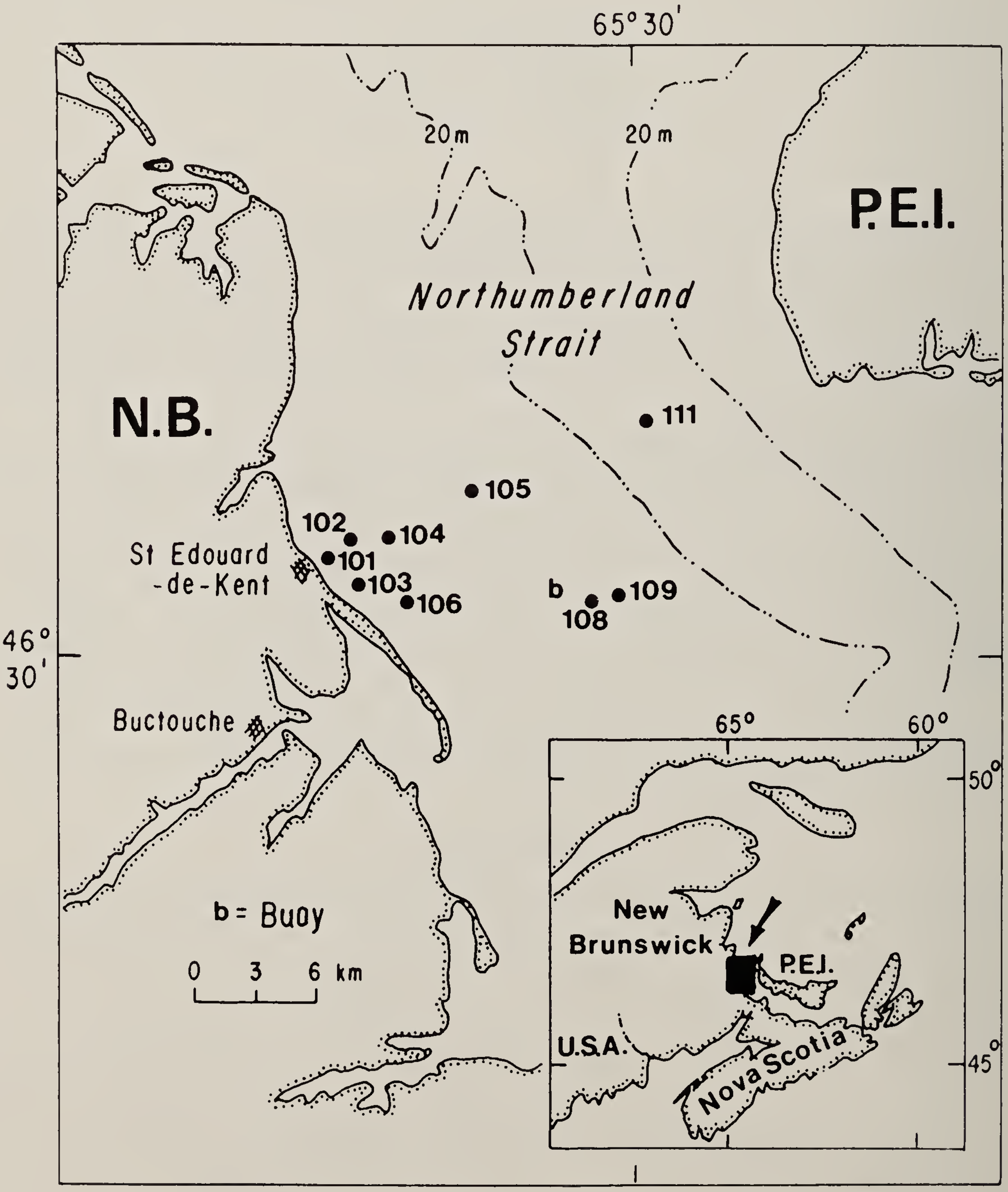

Fig 1. Location of sampling stations.

Crabs were preserved in 8% neutral formalin. Sex and carapace width were determined and intermoult stages were based on shell hardness determined by thumb pressure on the sub-branchial region, base of the legs, and telson (Haefner 1976). After a preliminary examination of approximately 50 crabs, 10 conspicuous epizoite categories were evident (Table I) and these were then used to assess epizoites on the sample of 6,145 crabs. Owing to their minute size and ubiquity, peritrichs, foraminifera, and diatoms, although usually present, were excluded from this analysis.

Seven large, hard-shelled crabs collected on May 26 were examined to determine the microdistribution of the overwintering epizoite species. A binocular microscope with ocular micrometer was used to examine the shells, and claws and legs were removed and examined individually.

Table I. List of 10 selected epizoite categories and their percent occurrence on 3,036 male and 3,109 female crabs.

Epizoite category	% Occurrence on males	% Occurrence on females
Ectoprocts	57.0	81.0
Tunicates	26.0	2.0
Hydroids	20.0	10.0
Bivalves	10.0	3.0
Limpets	1.0	1.0
Barnacles	0.5	0.7
Gastropods	0.5	0.4
Spirorbids	0.1	0.1
Amphipods	0.1	0.0
Anemones	0.1	0.0

Locations on the shell were defined by dividing the shell into 5 areas, each with 4 regions, and these in turn into 3 types of body surface. This generated a 3-digit code for all 66 potential locations (Table II; Fig 2), thus facilitating computer sorting and tabulation. Abundance, size, and location of epizoites were recorded and the epizoites removed and stored in 70% ethanol-5% glycerin for later identification.

Results

General Incidence of Epizoites

The mean widths of the 6,145 crabs examined (107 ± 10.6 mm for males and 84 ± 5.4 mm for females) are representative of commercial catches but not of the general population, due to selectivity of the traps (Stasko 1975).

Of the 10 selected epizoite categories (Table I), only the hydroids, ectoprocts, bivalves and tunicates were present on more than 2% of the crabs. The percent occurrence of these 4 epizoite categories (Fig 3) illustrates that ectoprocts were more common than hydroids, and these more so than bivalves. Tunicates ranked second to ectoprocts on males, but ranked lowest on females.

Seasonal abundance patterns of the 4 categories (Fig 4) show a rise in abundance of all 4 categories in late May followed by a decline in early June except for hydroids. From late June onward, for both males and females, ectoproct colonization increased and remained high. The percent occurrence of the other 3 categories remained stable except for an autumn peak of tunicates on male crabs.

Table II. Coding for designated locations on crab shells (also Fig 2). Each location was identified by 3 digits: area (1 to 5), region (1 to 4) and surface type subregion (0 to 2). For 7 crabs examined in detail, the total numbers of epizoite taxa, of the 53 identified, are recorded for each body location.

Area		Region	Number of Taxa/ Surface Type Subregion			Total Species/Area
			0 (Setae absent)	1 (Setae present)	2 (Indentation of surface)	
1. Dorsal	1—	carapace	7	0	3	14
	2—	eye socket	2	3	0	
	3—	antenna	3	1	0	
	4—	antennule	1	1	0	
2. Claws	1—	shell portion of segments	24	13	1	28
	2—	dactylus-propodus joint	6	9	0	
	3—	other joints	14	12	1	
	4—	coxal-thorax joint	0	1	0	
3. Legs	1—	shell portion of segments	19	22	2	29
	2—	dactylus-propodus joint	1	0	0	
	3—	other joints	12	7	0	
	4—	coxal-thorax joint	0	3	0	
4. Branchial chamber	1—	sub-carapace	1	0	0	4
	2—	gill	2	2	0	
	3—	hepatopancreas septum	1	0	0	
	4—	epidoites	1	3	0	
5. Ventral	1—	third maxilliped and buccal cavity	4	5	0	33
	2—	thoracic sterna and abdomen	4	3	0	
	3—	sub-abdominal thoracic area	0	0	0	
	4—	sub-hepatic and sub-branchial area	12	33	3	

Fifty-eight percent of males and 76% of females supported at least 1 taxon from the 10 categories. Nearly half of the crabs without epizoites were soft-shelled animals that had recently moulted. Of the crabs with epizoites, over 90% were hard-shelled accounting for 70% of all males and 84% of females. The maximum number of epizoite categories on individual crabs was 3 for females and 6 for males; 3 males had 5 categories and only 1 male had 6.

Microdistribution of Epizoites

Seven crabs collected in late May were thoroughly examined to determine diversity and distribution of epizoite taxa. Fifty-three taxa were distinguished, of which 35 were identified to species and an additional 7 to genus (Table III). The 53 taxa colonized 41 of the 66 potential locations (Tables II & III). Ectoprocts, coelenterates and polychaetes were the three most important categories in terms of numbers of species. *Alcyonidium polyoum* was the most widespread organism, occurring at 27 locations and on every crab. *Mytilus edulis* was almost as abundant, occurring at 26 locations. More than half the epizoite taxa were found only at 1 or 2 locations and on 1 or 2 of the 7 crabs. The number of epizoite taxa per shell location is shown in Table II. Ventral areas, legs, and claws supported the most species. Location 5-4-1,

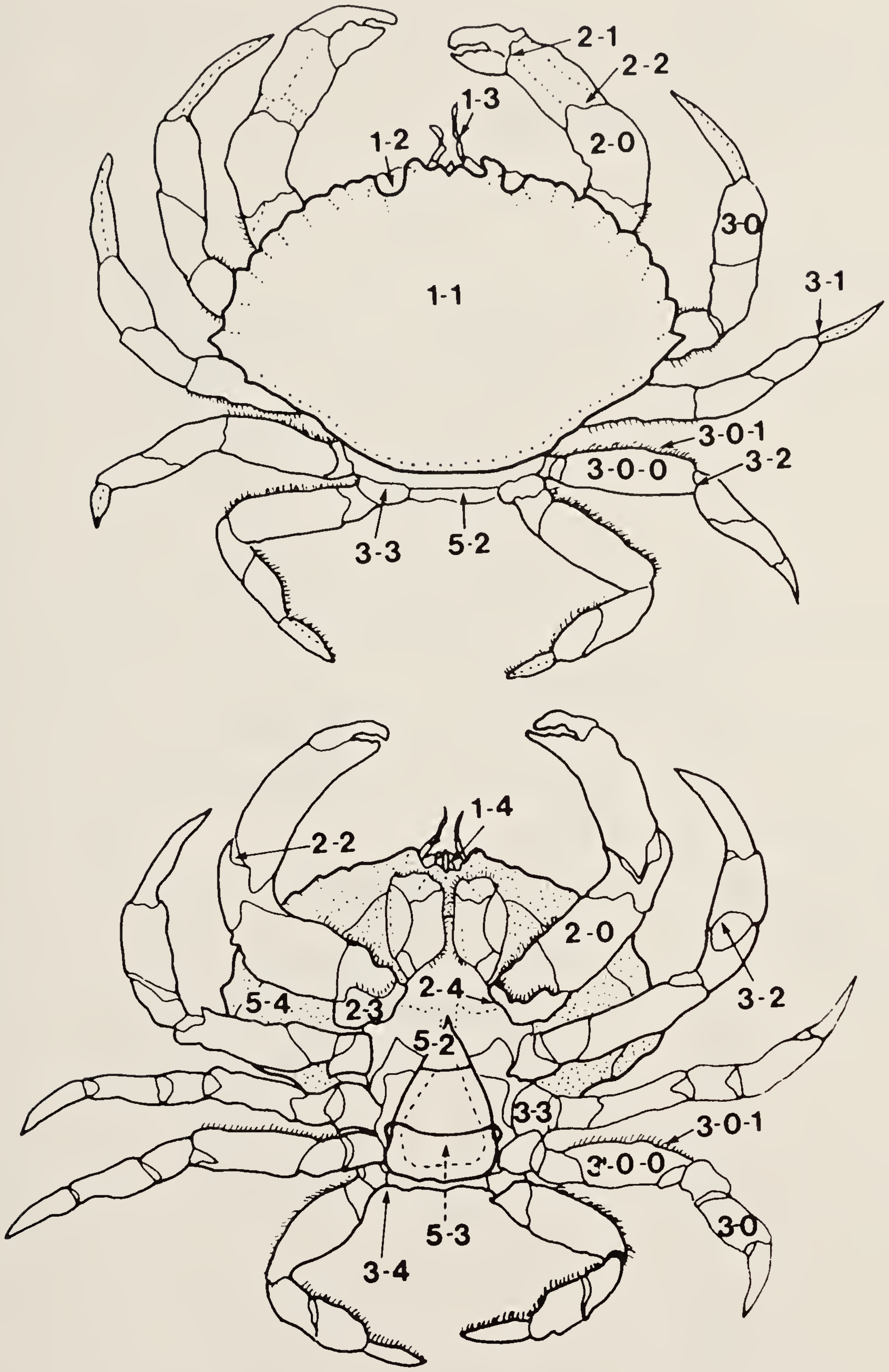

Fig 2. Dorsal and ventral aspects of *Cancer irroratus* depicting the shell areas, regions and surface type subregions, each denoted by one digit. The numbers of epizoite taxa found at each location are listed in Table III.

sub-hepatic and sub-branchial with setae, was richest, supporting 33 epizoic taxa. The branchial chamber had the least diversity: *Mytilus edulis, Alcyonidium polyoum, Obelia commissuralis* and a nemotode.

The top 2 or 3 most abundant epizoites from each major taxon (asterisk, Table III) were selected for further microdistribution analysis relative to shell substrate type (Table IV). In general, surfaces without setae favoured sessile organisms such as hydroids, barnacles and ectoprocts, while surfaces with setae favoured motile animals and nestlers such as mites, polychaetes, nematodes, turbellarians, and amphipods.

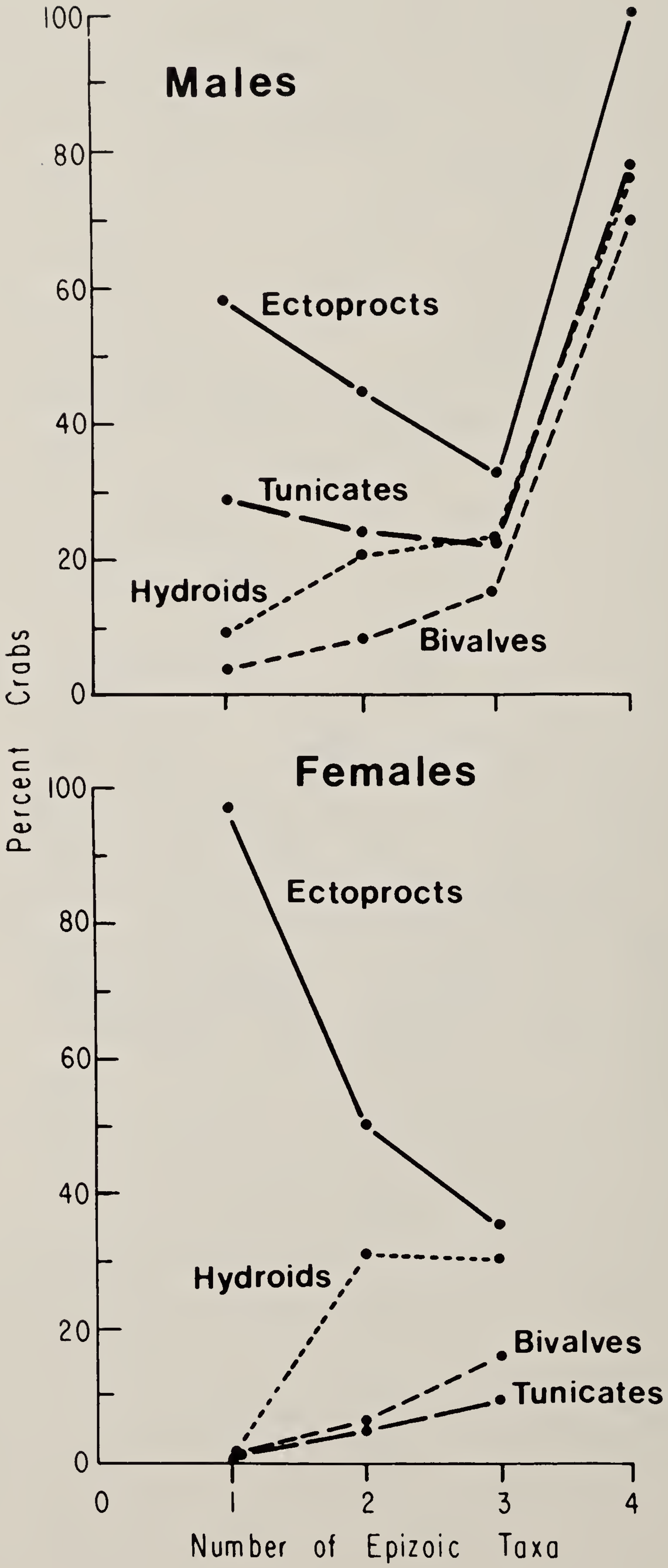

Fig 3. Percent occurrence on 3036 male and 3109 female crabs of the 4 major epizoite categories. Note that no individual females had all 4 categories.

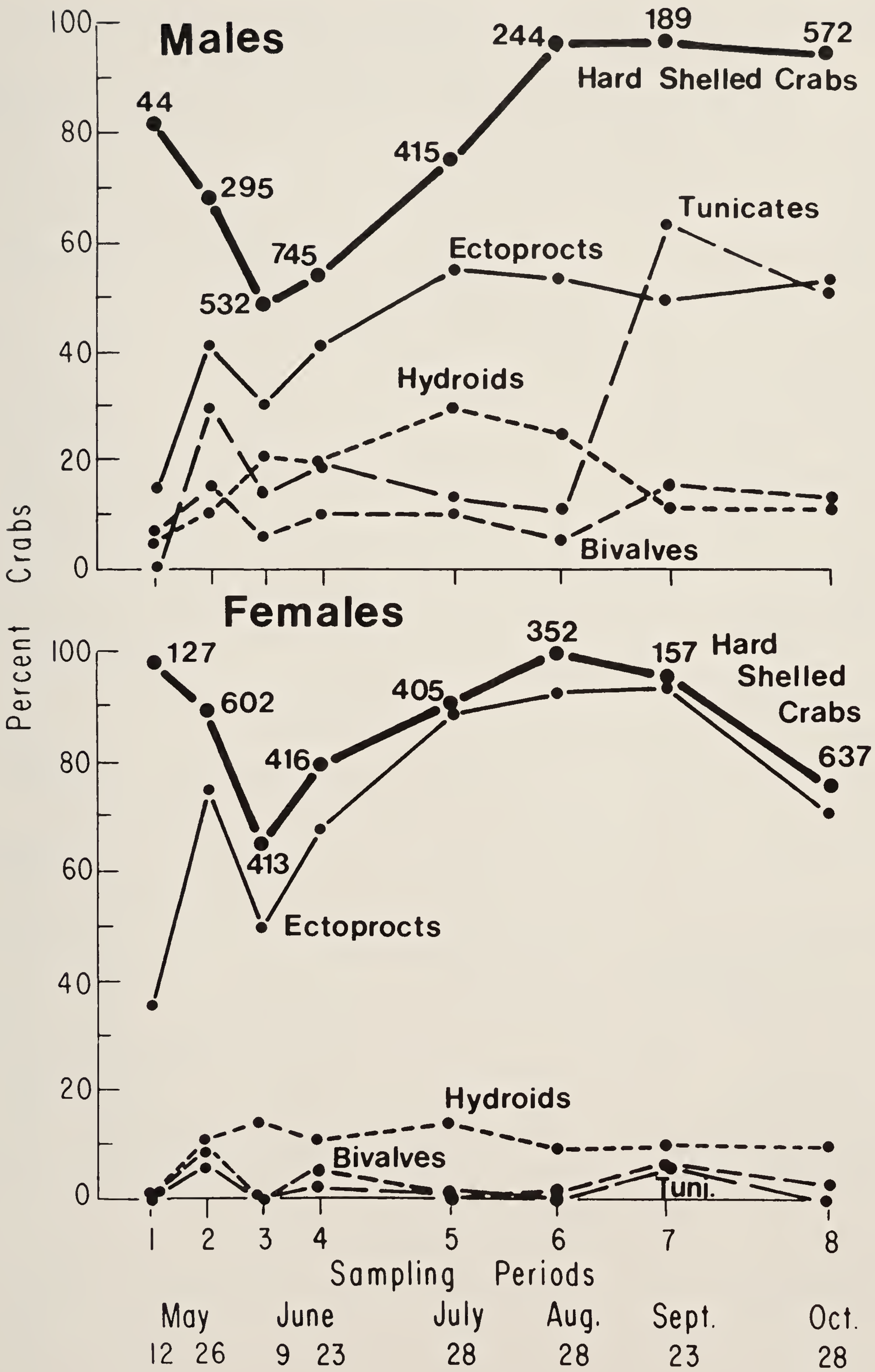

Fig 4. Relationship between seasonal percent occurrence of the 4 major epizoite categories and seasonal percent of hard-shelled crabs in each sample. Absolute numbers of hard shells for each date are indicated.

Table III. List of the 53 epizoite taxa and the number of crabs and locations colonized. Abundance is expressed as mm^2 for encrusting forms, as number of hydranths for erect hydroids, as number of zooids for ectoprocts and entoprocts, and as number of individuals for remaining epizoite species. Asterisk indicates 23 taxa included in a microdistribution analysis (Table IV).

Epizoic species	No. of crabs n=7	No. of locations n=66	Abundance
HYDROZOA			
Hydractinia echinata	7	11	1362*
Calyptospadix cerulea	7	21	1297*
Obelia commissuralis	6	14	836
Lafoea pygmaea	5	14	2183*
Thuiaria latiuscula	4	5	153
Calycella syringia	1	1	2
ANTHOZOA			
Actinaria (Tribe: Thenaria)	3	9	57
PLATYHELMINTHES			
Alloeocoela			
Plagiostomum sp.	4	9	30*
Egg cases	3	13	214*
ENTOPROCTA			
Barentsia sp.	1	1	12*
AMPHIPODA			
Corophium bonelli	2	2	4*
Proboloides nordmanni	1	1	1*
Gammaropsis sp.	1	1	1*
GASTROPODA			
Crepidula plana	1	1	2*
Crepidula fornicata	1	1	1*
Nitrella lunata	1	1	1*
Unidentified juvenile	1	1	1*
BIVALVIA			
Mytilus edulis	6	26	209*
Anomia simplex	3	2	12*
Hiatella arctica	2	1	2
Nucula sp.	2	2	2
Unidentified	2	2	2

Epizoic species	No. of crabs n=7	No. of locations n=66	Abundance
ECTOPROCTA			
Alcyonidium polyoum	7	27	43078*
Unidentified	5	10	718
Electra pilosa	5	7	1321*
Cribrillina punctata	5	5	121
Callopora aurita	2	5	143
Callopora craticula	2	4	32
NEMATODA			
Enoploidea	6	11	75*
POLYCHAETA			
Lepidonotus squamatus	5	7	11*
Polydora socialis	2	2	2
Circeis amoricana	2	1	5*
Polydora websteri	2	2	2
Capitella capitata	1	1	1
Nicomache lumbricalis	1	1	1
Terebellidae larvae	1	1	1
Unidentified sp. 1	1	1	1
Unidentified sp. 2	1	1	2
ACARINA			
Halacarus (*Thalassarachna* sp.)	6	9	37*
COPEPODS			
Pseudothalestris nobilis	1	1	1
OSTRACODA			
Unidentified	2	1	2
CIRRIPEDIA			
Balanus balonoides	3	10	123*
Balanoid cypris	3	6	17*
Haplota clavata	2	2	11
Electra monostachys	1	4	213
Parasmittina sp.	1	2	132
Stomachestosella sinuosa	1	2	70
Tubulipora sp.	1	2	9
Lichenopora verrucaria	1	1	32
Tricellari peachii	1	1	1
Crisia eburnea	1	1	1
Tegella unicornis	1	1	10
ASCIDIACEA			
Molgula citrina	5	6	41*

Table IV. The 23 epizoite taxa, found on 7 crabs, grouped according to percent occurrence on each of the 3 types of body surface. No epizoite had its greatest abundance in subregion 2.

Epizoite species	Body Surface Subregion 0 (Setae absent)	 1 (Setae present)	 2 (Indentation of surface)
1) Abundance greatest in subregion 0			
Hydractinia echinata	90.1	9.9	0
Lafoea pygmaea	61.3	38.4	1
Alcyonidium polyoum	95	4	1
Electra pilosa	99.3	1.7	0
Circeis amoricana	100	0	0
Balanus balanoides (adult)	90	9	1
Balanus balanoides (cypris)	88	6	6
2) Abundance greatest in subregion 1			
Actinaria (Tribe: Thenaria)	33	65	2
Calyptospadix cerulea	31	69	0
Plagiostomum sp. (adult)	36	64	0
Plagiostomum sp. (egg cases)	46	54	0
Barentsia sp.	0	100	0
Nematode	11	87	0
Unidentified ectoproct	19	81	0
Lepidonotus squamatus	27	73	0
Halacarus (Thalassarachna) sp.	12	88	0
Amphipoda: 3 spp.	14	86	0
Gastropoda: 3 spp.	25	75	0
Anomia simplex	27	73	0
Mytilus edulis	28	72	0
Molgula citrina	10	90	0

Discussion

Relative to similar studies on decapod crustacean epizoites (Table V), *Cancer irroratus* from Northumberland Strait is exceptional in supporting 53 taxa of macroinvertebrates.

Crabs for the microdistribution analysis of epizoite species were collected in May so as to represent the overwintered epizoites before the spring moulting. Sampling later in the year might yield higher species densities or more recently settled species, but would not indicate competitive species capable of surviving through the intermoult period.

Seasonal abundance patterns of the 4 most abundant groups reflected the moulting periods of the host. When large numbers of recently moulted crabs were caught in mid-June (Fig 4) the percentage of crabs colonized by epizoites decreased. However, at the end of May there was an increase in all epizoite groups at a time when the percentage of hard crabs decreased. This indicates a period of rapid growth and/or settlement of epizoites.

The ectoprocts, especially *Alcyonidium polyoum*, are excellent indicator species of intermoult stages because of their rapid rate of colonization. They were the only epizoite group occurring on females at a higher frequency than on males, thus accurately reflecting the fact that a larger percent of females were hard-shelled.

In the present study, the 23 species whose microdistribution was examined were most influenced by the presence or absence of setae. This distribution is largely a reflection of the organisms' tolerance to accumulation of detritus. Low-profile encrusting ectoprocts are generally intolerant of sediment buildup (Hughes 1975) and regions which possess setae accumulate detritus since setae serve primarily as strainers (Pearson 1908). With a buildup of detritus, a suitable microhabitat is created for motile species such as turbellarians, amphipods and polychaetes. Thus setae serve a structural function analogous to sessile organisms of the general fouling community, which have been considered to be a pre-requisite to the establishment of motile animals (McDougall 1943).

Mytilus edulis and *Alcyonidium polyoum* were the only deleterious epizoites found in this study. Within the branchial chamber *M. edulis* caused considerable distortion of gill lamellae, as well as sediment accumulation. Where it occurred in the eye socket and at limb joints, movement of appendages was restricted. *A. polyoum* also grew in the branchial chamber, on both gills and epipodites. Both species lower respiratory efficiency and increase the risk of tissue damage and infection. To our knowledge, *M. edulis* has not previously been reported growing on *Cancer irroratus* or any other crustacean.

Table V. Number of epizoite species on crustacean hosts reported in previous studies.

Host species	Epizoite species	Reference
Homarus americanus	15	Dexter (1955)
Callinectes sapidus	9	Pearse (1947)
Porcellana platycheles	6	Smaldon (1974)
Porcellana platycheles	5	O'Donohue (1935)
Callinectes sapidus + 13 other spp.	5	DeTurk (1940)
Cancer irroratus	5	Terretta (1973)
Cancer irroratus	5	Haefner (1976)

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OVINE ILL-THRIFT IN NOVA SCOTIA
6. QUANTITATIVE DESCRIPTION OF THE FUNGAL FLORA OF SOILS OF PERMANENT PASTURE*

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Four hundred thirty-seven soil samples were collected from upland pasture at Nappan, Nova Scotia between April 24 1967 and October 28 1975. From these soil samples 5605 fungal isolates were established in culture. The mean value for the number of fungal propagules per g of dry soil was 8.2×10^5 and this value remained the same over the experimental period of 9 yrs. One hundred forty-two fungi have been classified, 137 belong to known genera, of which 54 are known species. The isolates classified into these 142 fungi constitute 35% of all isolates. The isolates collected in 1967, 1968, and 1970 were not available in 1978 mainly because of loss of viability. The remaining 2683 isolates, collected between May 5 1969 and October 28 1975 had characteristics similar to those of the whole collection. Methods of selecting random samples of 750 isolates were investigated. Tests were devised to compare these random samples with the total population and used to select a sample that appeared to be most representative. The mean number of fungal propagules/g of soil in this sample was 4.8×10^4 and this number remained unchanged throughout the experimental period. Sixty-seven fungi from the representative sample have been classified and these constitute 49% of the different isolates in the sample. All of these isolates (543) were tested for their ability to produce metabolites that inhibited the growth of *Sarcina lutea* and/or *Candida utilis*. The growth of both organisms was inhibited by 3% of the isolates; 24% of isolates inhibited the growth of only *S. lutea* and 3% affected only *C. utilis*.

Introduction

A number of difficulties attend a quantitative description of the fungal flora of a soil sample. The flora may be an interlaced web of mycelium on the one hand or a dense packet of spores on the other, but it is generally somewhere between these two extremes. It is therefore hard to assess whether 2 or more fungal colonies, isolated by any means, are derived from the same or from different organisms, unless they are different species. It has therefore been argued (Ainsworth 1968) that enumeration of a soil fungal flora is meaningless. To assess the population density of a fungal flora, the concept of a fungal propagule has arisen (Brierley et al. 1927) but the term is used differently by different workers. As it is essential to our attempts to describe the flora of permanent pasture, we define our use of the term. It is clear that dispersion of the soil matrix involves disruption of delicate living tissues such as root hairs, fungal mycelium, chains of bacteria, etc. If the cell contents are spilled in this shearing and grinding process, regeneration is unlikely. Hence, anything cultivated from the dispersed biomass arises from an essentially intact cell, be it spore, hyphal fragment, chlamydospore, etc., likely surviving structures are highly dependent on individual species. It might, therefore be expected that surviving viable entities will range from single cells, e.g. spores, to hyphal fragments (Kliejunas & Negata 1979) and further to intact conglomerations of cells, e.g. sclerotia, or even interwoven strands of hyphae from mycelial mats. Regardless of their morphology, such varied viable units may grow in cultivation and result in a discreet colony. We use the word "propagule" to delineate a fungal fragment isolated by a process such as that described; the process, method of dispersion, temperature of cultivation, and nutrient medium all being defined (Brierley et al. 1927). It is now possible to examine the questions: is the number of such propagules related to the density of the fungal flora of a soil sample; can this relation be determined, and if so, with what precision?

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During the isolation procedure, provided normal sterility techniques are used, there are no additions to the flora. However, at the moment of isolation, metabolic and mechanical modifications of the flora start. These modifications result in the loss of propagules, by disruption, digestion, aeration, and/or dilution. The number of species in the soil defines the lowest possible number of fungal organisms therein. The greatest number of fungal organisms is also defined by the volume representing the difference between that of the hydrated ash and unit volume of soil divided by a hypothetical mean cell volume. The size of the interval thus defined is probably much smaller in practice. Many fungal organisms are present as single cells and at the other end of the scale much of the biomass may not be part of the fungal flora. It is evident that there is a probability function with a maximum value, that gives the chance of finding a number of fungal organisms in a particular soil sample. The position is similar to that of a fundamental particle whose position is described by a probability function, the uncertainty not precluding predictions about its role in the properties of matter. Similarly, the smallest possible number of fungal propagules that it is possible to isolate is the number of surviving species and the maximum number is the same as that defined above for the maximum number of fungal organisms present. The interval is therefore wider than that of fungal organisms but the probability distribution is displaced downwards because of the loss of fungal tissue in the isolation procedure. It follows that the probablility functions of the two concepts—fungal organisms and fungal propagules—will be similar, with a high probability that the maximum of the latter will lie at a smaller value than that of the former. A similar argument can be applied to any other concept of the fungal flora, e.g. the number of cells. The foregoing describes the fraction of the soil flora theoretically available for study by means of some dispersion and isolation process. There remain two other matters to be discussed before proceeding to report the results of our experimental work.

In the foregoing analysis, the concept of species has been used as a limit. Historically, classification of fungi has been based on their morphology with particular reference to structures elaborated during reproduction. In the case of parasites, and to a lesser extent symbionts, the discrimination of hosts or partners has played a role in fungal classification. This system of classification has its disadvantages when studying the ecology of fungi from a habitat in a more or less comprehensive fashion. Many fungi, with known teleomorphs, produce only their anamorph in culture and it is often difficult to relate the culture to the known teleomorph. It is also possible for the anamorphs of different teleomorph species to be grouped into the same species aggregate (Rifai 1969). The existence of the parasexual cycle (Pontecorvo et al. 1953) in the Deuteromycotina leads to the possibility of isolates of the same anamorph species having conspicuously different characteristics. Also, anastomosis of hyphae of supposedly different species provides new heterokaryons often difficult to assign. A further problem stems from the objective—to describe all the fungal isolates, large numbers of which may produce no morphological feature that is characteristic in a classical sense. These difficulties suggest that a numerical system of classification might be useful. However, numerical systems of taxonomy traditionally have been applied to relatively uniform groups, usually bacteria, but a wide diversity of organisms is found in the soil fungi. Hence, we have adopted a numerical key, each isolate having similar, recognizable characters being assigned a number. In some cases, these characters were sufficient to classify the organism with respect to genus and in others, species. The system has the disadvantages that it has no logical or mnemonic properties.

Faced with the object " . . . . . ", most would agree that it contained 5 periods, but if about 5000 periods were to be counted on 2 or more occasions, greater difficulty would be found in arriving at the same total. If, therefore, it was possible to disperse 1 kg of soil it would be unlikely that 2 or more mycologists would count the same number of fungal colonies grown therefrom in culture. But it follows from the analysis given, that a large number of soil samples must be counted to arrive at a reliable estimate of the number of fungal propagules in a given weight of soil. This Herculean task is evaded by counting the colonies grown from about 50 μg of soil, but then it is difficult to be sure that the soil samples are representative, and that distortions do not occur in extrapolation of the results to the soil of a useful area of land, e.g. a hectare. We have tried to overcome these problems by collecting a large number of soil samples in a random distribution over the experimental area. The samples have been collected over a period of 9 years and the fungi have been isolated by setting up 10 replicates of a dilution series of each soil sample (Montegut 1960).

Problems in counting and sorting have been overcome by the use of a computer, and this aid has also allowed the expansion of collections to reflect their frequency in the field. The algorithms used are simple and inelegant, but are given in the hope that other mycologists will use and develop them.

Methods

Experimental Plot

The experimental plot (P2, Brewer et al. 1971) was located at the Agriculture Canada Experimental Farm, Nappan, Nova Scotia. The boundaries of the plot in 1967, 1968, and 1969 were those described by Brewer et al. (1971), but only colltions from the sectors specified below are included in the data used in this paper. From and including 1971 the plot was essentially sectors C and D in 1967 and 1969, and sector B in 1968, but extended eastwards towards the wooded area and westwards towards the bull-barn. A detailed map is given in Figure 1. The extensions of the plot did not introduce additional plant species, areas of different husbandry nor different soil types. For the collection periods 1973 to 1975 inclusive the plot was divided into 10 equal sectors as shown in Figure 1. In other years, when calculations required sector specification, a random number (1-10) was generated for each soil sample during the calculations. Collections were made approximately at noon, at random over the area of the plot, by generating random numbers for each collection date, the numbers referring to a section of the plot. Additional randomization was ensured by using about 20 people to collect the samples over the 9-year period. The method of collecting the soil cores was described by Brewer et al. (1971) where the number and times of collection in 1967, 1968, and 1969 are also given. In 1970, 28 soil cores were collected on 15 days at about weekly intervals between May 12 and August 20. In 1971, 7 soil samples were obtained at monthly intervals from April 27 to October 25. Sixty-four soil cores were collected in 1973 on 26 occasions, at roughly weekly intervals between May 2 and October 28. In 1974, 50 soil samples were obtained on a weekly basis between May 6 and June 3, and from June 17 to October 29. Fifty-two soil samples were collected in 1975 at 26 weekly intervals from May 6 to October 28. The total number of soil samples collected, from 1967 to 1975, was 437, on 167 collection dates.

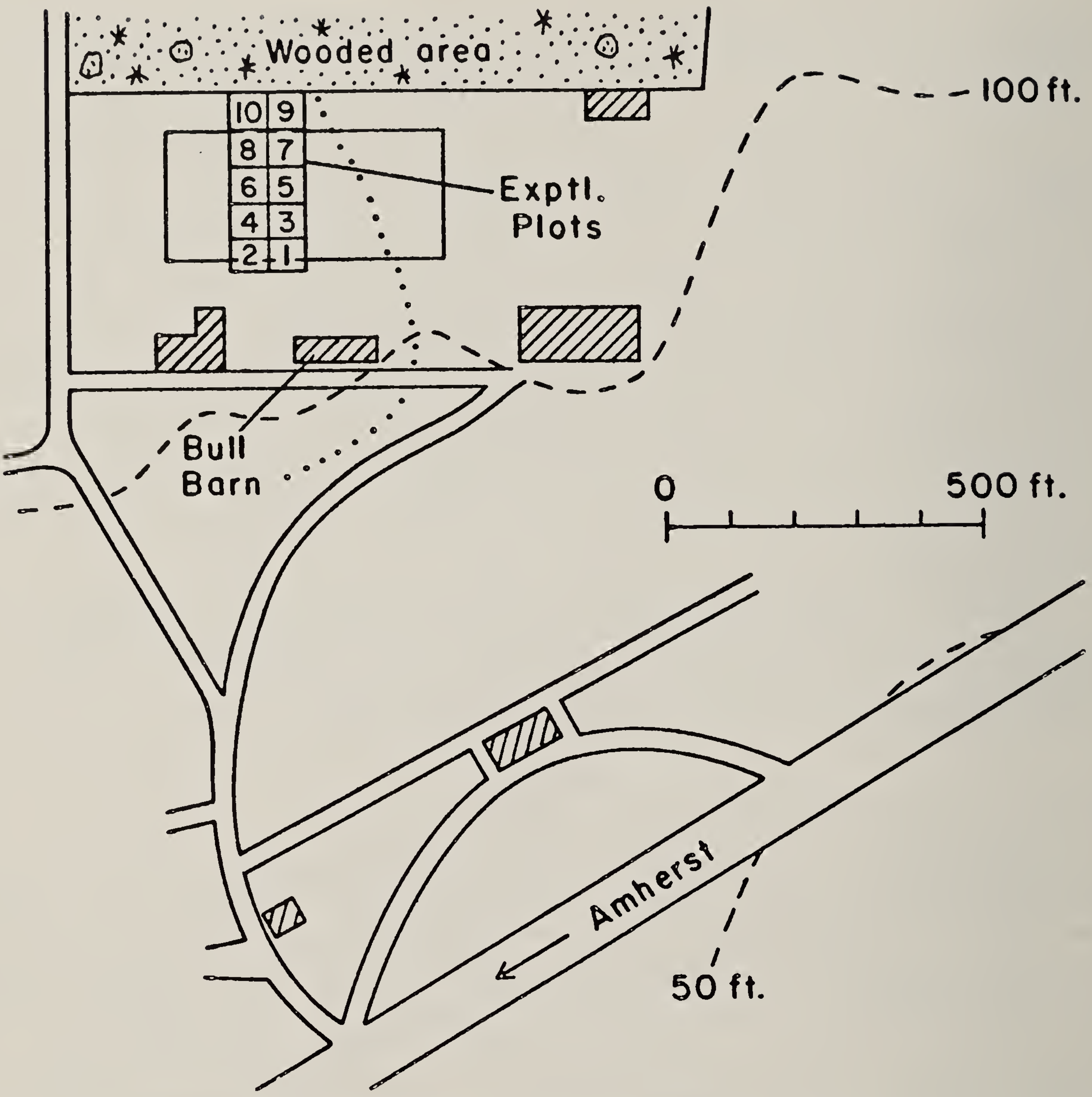

Fig 1. Location of the experimental plots. The area divided into 10 numbered sections is the plot used to collect soil samples described in this paper. The larger area in the same locality was the area used to collect soil samples described by Brewer et al. (1971).

Isolation of Fungal Propagules

In the years 1967 to 1972 inclusive, fungal propagules were isolated as described by Brewer et al. (1971). From 1973 to 1975, a laboratory was available adjacent to the experimental plot and dilution series were made within 1 hour of collection of the soil sample. In the 2 latter years, the medium used to cultivate the fungal propagules was augmented by addition of soluble starch (1 g l^{-1}) and cellulose (6 g l^{-1}, MN300, Nagel & Co.). The plates were incubated for 7 days at 25°C and the numbers of fungal colonies appearing were counted. A subculture onto 2% (w/v) malt agar was made of each of the colonies that appeared to have characteristics that differed from others on the plate. A record was made of the number of colonies of each type occurring on 10 plates from which it was isolated, the ability to hydrolyze starch and cellulose, the ability to reduce rose bengal, and the growth-inhibiting effect (if any) on adjacent fungal colonies. When doubt occurred as to whether or not one colony was truly different from another, subcultures were made from both. In 1979, those organisms collected in 1969, 1971, and 1973 that remained viable were subcultivated onto the starch-cellulose medium, and their ability to reduce rose bengal and hydrolyze the polysaccharides was recorded.

Numerical Formulation of Ecological Data

The system developed to translate fungal ecological data into numerical code, had as its basic condition that one line of ciphers was assigned to each isolate. The following criteria were used in devising the code: each line had to be unique, with mnemonic properties, i.e. it could be deciphered without recourse to a key; the code should appear in groups of ciphers that were code for related phenomena, to ease sorting problems; and finally, the code should be compatible with readily available peripheral machinery associated with computers. It was also desirable, though not essential, that the code should be written in a way that made its use in computational devices as efficient as possible, thus reducing the time required for calculations. When (1970) we decided to translate our field observations into such a code the computer facilities available to us imposed the following restrictions. Only 6 digits could be used for input and output of integral numbers; no line could be more than 72 characters; integral numbers were most efficiently stored in groups of 4; and processing of numerical data was several orders of magnitude faster than text. Most of these restrictions have now disappeared, but only minor modifications of the code have been made, thus improvements in computers have merely increased the speed of processing. Each fungal isolate can be uniquely described by the date of collection of the soil sample from which it was cultivated, the geographical location of the collection site and a number assigned to each different isolate on a group of 10 dilution plates. As collections were made in the period 1967 to 1975, the year of collection can be represented by the last digit of the year number A.D., i.e. 7 to 5, and as collections were only made each year between April and October, these months can be indicated by the numbers 4, 5, 6 . . . 0. The number 224309416 thus uniquely describes fungal isolate number 16 cultivated from a soil sample collected from sector 4 of plot 9 on April 22 1973. The number had to be broken into the parts 224309 and 416 because of the restrictions mentioned. This division leaves 3 digits in the second group, i.e. 416xxx, and these have been used to indicate the frequency of this particular isolate in terms of numbers of propagules in 1 g of dry soil. This number was recorded to 2 significant figures, the last digit being used to record the power of 10 to which these significant figures should be raised. Thus the ciphers 274 indicate that the frequency is 27,000 g^{-1}. The third and fourth groups of ciphers have been used to record taxonomic, physiological and meteorological information concerning the isolate. Each of these subjects is discussed separately.

Taxonomy

No attempt has been made to devise a systematic numerical code for classified soil fungi. Initially it was considered unlikely that more than 9999 species would be found, thus the 4 left-hand digits in the third group were assigned for taxonomic classification. It was also thought that it might be possible to reserve the second and third ciphers from the left to indicate genus, and this has been done in several instances but, in general, has proved to be too complex to retain in mind. Rather, it was easier to construct and augment a separate file of species and their assigned numerical code (Brewer et al. 1978).

Physiology

Most of the physiological information observed on these fungal isolates was obtained after considerable development of computer machinery. In particular, the restriction of 6 digits disappeared. Thus, physiological data have been written in code in the third group of digits. The data are of 2 kinds. First, there is information read directly from the isolation plates, viz., does the colony reduce rose bengal; is it surrounded by a clear zone in the opaque cellulose agar or is there a zone around the colony that does not give a blue colour with iodine? Finally, does the colony inhibit the growth of an adjacent colony and if so which? The code used to record these data is as follows (digital place numbers are counted from right to left): in the fifth place the zone of starch hydrolysis is given as the difference between the zone diameter and the diameter of the colony divided by 2. The sixth place is assigned the value of 1 or 0 according to whether rose bengal is reduced or not and the seventh place is given the same values (1 or 0) if cellulose hydrolysis is or is not observed. The eighth place is assigned the isolate number of the colony whose growth is inhibited, the value 0 indicating that no growth inhibition was observed (the cipher 9 was used to indicate growth inhibition of several isolates). Ciphers in the ninth (and greater) place indicate data of the second kind i.e. experimental results obtained on isolates after they had been admitted into the culture collection. Numbers in the ninth place indicate the following: 1, activity against *Sarcina lutea* (HLX 701*); 2, against *Candida utilis* (NRRL Y900); 3, against both; and 9 indicates activity in the screen reported by Brewer et al. (1972). Thus the ciphers 181130178 indicate an isolate of *Trichoderma hamatum* (0178) which hydrolyzes starch (zone radius 3 mm), reduces rose bengal, hydrolyzes cellulose, inhibits the growth of isolate 8 collected in the same soil sample and also of *S. lutea*.

Meteorology

Meteorological data were stored in the fourth group of ciphers. The 2 digits on the extreme right record the rainfall in millimeters in the 7 days prior to the collection of the soil sample, the third and fourth digits record the temperature of the soil at collection time 5 cm below the surface, and the fifth and sixth digits record the temperature of the soil 1 cm below the surface. The seventh place in this group of ciphers has been used to indicate whether or not the isolate has been selected in a random sample upon which taxonomic and/or physiological studies have been done. The number inserted in this seventh position indicates the number of times the isolate was selected in the frequency-weighted random sample. Thus the group of ciphers 2181604 means that there were 4 mm of rain in the week prior to collection, that the temperature of the soil at the collection site at the time of collection, 5 cm below the surface, was 16°, at 1 cm below the surface 18°, and that 2 entries of this isolate appeared in a random sample from which additional information has been obtained. To summarize, the line 224309 416274 181130178 2181604, taken from the examples given, uniquely describes the fungal propagule and condenses much information about it in a line of code easily deciphered.

Construction of Computer Files of Fungal Ecological Information

The conversion of field and laboratory observations into code described in the preceding section and the assembly of these data into files of information is a tedious job that has a high risk of human error. Several methods of doing this job were tried and the following was found to be susceptible to fewest errors. It is, therefore, described in detail. One page, divided into 16 columns, of an 8 x 11-in hard-backed book was used for each soil sample collected. The day, month, year, plot number and sector number were written into the first 5 columns from the left at the time of collection of the soil sample. At the same time, the temperature of the soil adjacent to the collection core at 1 cm and 5 cm was entered into the seventh and eighth columns and the rainfall into the sixteenth. When the cultures were examined after 7 days incubation, the different colonies were given an isolate number 1 to n, and this number was inserted into column 6, the combination of the numbers in columns 1-6 then being used to identify subcultures. These field books thus served as an accession catalogue to the growing collection of fungal isolates. At the time of isolation the following data were also entered into the field books: the number of identical colonies on the 10 plates was inserted into column 9 and the dilution of the soil sample represented by the 10 plates into column 10. The isolation number of another colony (if any) that was inhibited was entered into column 12, starch and cellulose hydrolysis in columns 13 and 14, and rose bengal reduction in column 15. If the taxonomic code was known, it was entered at this stage into column 11.

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*Accession number to the collection of micro-organisms held at this laboratory.

The data in the field books were then recorded on magnetic tape using a computer terminal (e.g. Texas Instruments silent 700) equipped with a cassette recorder. Each line in the field book was typed as 1 line of data on the tape starting with a line number (2000 increasing by 1 for each line) and then the word "data". This method has the advantages that the data can be checked and errors corrected before transmission to the computer via acoustic coupler and telephone line, and the tapes are a valuable copy of the data in the field books. The computer program given in Appendix A can also be recorded on the tape and then all the information transmitted to the computer. The commands required to do this job, to execute the program and to store the program but not the data, differ from one computer center to another, but are simple and will be explained to potential users by the staff of such institutions. All computer programs used in this work were written in the beginners all-purpose symbolic instruction code (BASIC). An annotated listing on the program used for expanding a collection of isolates to reflect their frequency and for selecting a random sample of 750 of the expanded collection is given in Appendix B. Duplicate copies of files of field data were kept on standard 7-track magnetic tape. One of these was kept at the computer center and the other in the laboratory. As new information, e.g. taxonomic, became available it was added to the files on the 7-track tapes by using facilities available at the computer center. At the beginning of this work programs were written to edit these files; these programs and all others used in this work are available on cassettes from the Librarian of the Nova Scotia Institute of Science should they be thought to be of use to other mycologists. All computations were done using Control Data Corporation computers.

Antibiotic Assays of Cultures of Soil Fungi

Giant colonies of the fungi screened for the production of antibiotics were grown as described by Brewer et al. (1972). The assay procedure was as described by Brewer et al. (1974), employing *S. lutea* and *C. utilis*, except that the dishes inoculated with *C. utilis* were incubated at 25°C for 42 h.

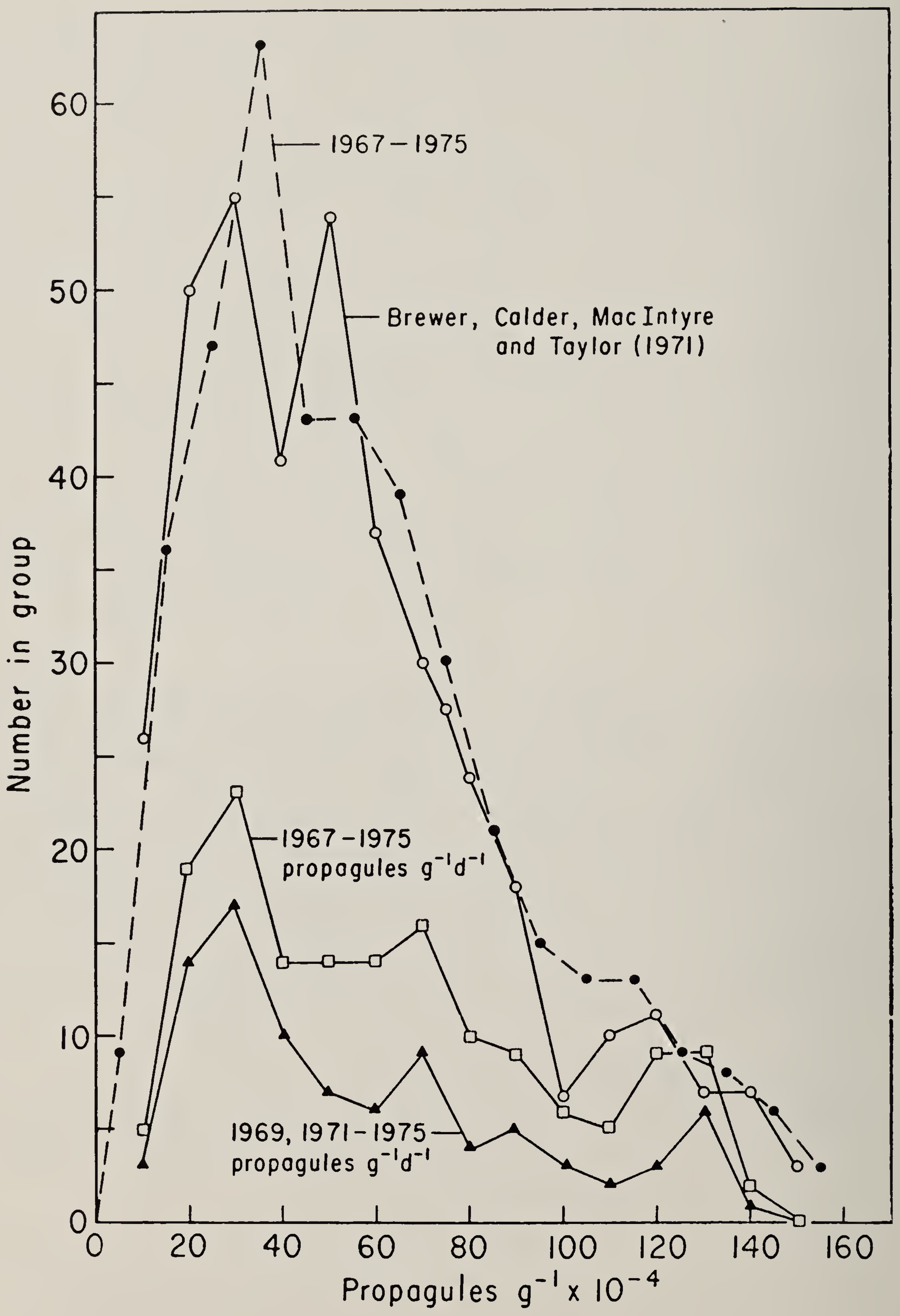

Fig 2. Numbers of soil samples collected from which fungal propagules were cultivated (groups of 10^5).
In the period 1967 to 1975 there were 39 samples collected for which values exceeding 1.55 x 10^6 propagules g^{-1} were obtained. In the period 1967 to 1975 there were 12 occasions when the mean value for the collection date exceeded 1.6 x 10^6 propagules g^{-1} and in the period 1969, 1971 to 1975 there were 8 occasions.

Table I Mean numbers of fungal propagules in 1 g of dry soil collected from different sectors of a plot of permanent pasture in 1973 to 1975.

Sector	No. of soil samples collected	Propagules g^{-1} (x 10^{-4})			
		Max.	Min.	Mean	Standard deviation
1	15	33	2.7	12	25
2	10	26	2.3	9.4	24
3	18	130	2.2	14 (6.7*)	37
4	18	22	1.2	8.2	15
5	13	29	0.6	9.0	21
6	18	63	0.9	11.	27
7	22	15	0.7	5.6	8.5
8	16	17	1.3	5.0	10
9	19	11	0.9	4.5	0.8
10	11	32	2.1	9.4	23

*Omitting one collection of 10^{7} g^{-1}

Results

Characteristics of the Fungal Flora of the Soils of Permanent Pasture

Brewer et al. (1971) reported that the mean value of fungal propagules g^{-1} for 423 upland (forest) soil samples collected in spring, summer and fall of 1967, 1968, and 1969 was 6.04 x 10^{5}. They gave a histogram of the numbers of soil samples collected from which fungal propagules (in groups of 10^{5}) were cultivated. This histogram is reproduced in Figure 2. A very similar number of soil samples (437) was collected from part of the same plot (Fig 1) but over a longer period of time (1967-1975). The mean number of fungal propagules g^{-1} of dry soil in this set was 6.9 x 10^{5} if one collection of 1.3 x 10^{7} is omitted. A histogram of these 437 soil samples is given in Figure 2; both groups of data are clearly similar. The mean numbers for each month of the growing season in the 1967-1975 data were as follows (soil samples collected each month in parentheses): April, 5 x 10^{5} (17); May, 6.9 x 10^{5} (73); June, 6.8 x 10^{5} (73); July, 6.9 x 10^{5} (92); August, 6.5 x 10^{5} (65); September, 7.5 x 10^{5} (55); October, 7.3 x 10^{5} (62), omitting a single value (1.3 x 10^{7}) collected in July. The standard deviation of the means is 8.2 x 10^{4} and hence, as in earlier work (Brewer et al. 1971), there was no significant difference in the number of fungal propagules cultivated from soil samples collected in the annual period April to October inclusive. In general, more than one soil sample was collected on each of the 167 collection dates in the period 1967-1975. The mean value of propagules g^{-1} obtained on each of these collection dates was calculated, and the numbers obtained sorted into groups of 10^{5}. The resulting histogram is drawn in Figure 2. The group containing the maximum number of collections (3-4 x 10^{5}) is the same as in the other histograms in Figure 2. The mean value for all 167 collection dates was 8.2 x 10^{5}. The dates of collection were converted into a time scale—April 24 1967 = day 1, October 28 1975 = day 3108 and the mean propagules g^{-1} for each of the collection days used as 167 data points to calculate a linear least mean squares fit. The gradient of the fitted line was 22 and the difference, therefore, between day 1 and day 3108 was 6 x 10^{4}. Hence no significant change in propagules g^{-1} isolated occurred in the 9 years. No differences in the

Table II. List of fungi isolated from soil samples.

Organism	Mean no. of propagules /g soil	No. of soil samples	No. of isolates in collection	Observed optimum temperature range* (°C)	Calculated optimum temperature (°C)
Absidia	62,000	2	2	17-20	
Absidia coerulea Bainier	22,000	7	8	25-28	
Absidia corymbifera (Cohn) Sacc. & Trotter	38,000	1	1	25-28	
Absidia glauca Hagem	27,000	20	21	17-20	18 (17)
Absidia spinosa Lendner	15,000	2	2	17-20	
Acremonium	6,000	1	1	5-8	
Alternaria	32,000	1	1	17-20	
Alternaria alternata (Fr.) Keissler (461)	7,000	1	1	21-24	
Alternaria alternata (462)	19,000	3	3	21-24	
Aspergillus	125,000	2	2	25-28	
Aspergillus chevalieri (Mang.) Thom & Church	5,000	1	1	13-16	
Aspergillus chevalieri var. *intermedius* Thom & Raper	34,000	3	3	25-28	
Aspergillus fumigatus Fresenius	7,000	2	2	21-24	
Aspergillus sydowi Bain. & Sart.	36,000	1	1	9-12	
Chaetomium	17,000	7	7	9-12	
Chaetomium funicolum Cooke	12,000	1	1	13-16	
Chaetomium umbonatum Brewer	19,000	11	13	17-20	(17)
Circinella	10,000	1	2	13-16	
Cladosporium cladosporioides (Fresen.) de Vries	78,000	10	10	21-24	
Cladosporium herbarum (Pers.) Link ex S.F. Gray	31,000	9	9	21-24	(21)
Cunninghamella	28,000	8	11	17-20	
Cunninghamella elegans Lendner	71,000	1	1	25-28	
Curvularia protuberata Nelson & Hodges	20,000	1	1	21-24	
Cylindrocarpon destructans (Zins.) Scholten	17,000	3	3	13-16	

Organism	Mean no. of propagules /g soil	No. of soil samples	No. of isolates in collection	Observed optimum temperature range* (°C)	Calculated optimum temperature (°C)
Diheterospora chlamydosporia (Kamyschko) Barron & Onions	68,000	7	7	25-28	
Eladia saccula (Dale) Smith	26,000	5	5	13-16	
Fusarium	26,000	64	74	17-20	19 (18)
Fusarium avenaceum (Corda ex Fr.) Sacc.	31,000	2	3	17-20	
Fusarium culmorum (W.G. Smith) Sacc.	61,000	1	1	17-20	
Fusarium oxysporum Schlecht.	15,000	13	13	17-20	
Fusarium poae (Peck) Wollenweber	45,000	4	5	25-28	
Fusarium solani (Mart.) Sacc.	29,000	38	44	17-20	20 (18)
Gliocladium	32,000	2	2	17-20	
Gliocladium atrum Gilman & Abbot	21,000	3	3	13-16	
Gliocladium deliquescens Sopp	13,000	4	4	29-32	
Gliocladium roseum Bain.	58,000	114	149	17-20	19 (18)
Gongronella butleri (Lendn.) Peyronel & Dal Vesco	91,000	122	129	13-16	19 (17)
Gymnoascus roseus (Raillo) Apinis	15,000	6	6	9-12	
Humicola grisea Traaen	26,000	6	6	25-28	
Metarrhizium anisopliae (Metsch.) Sorok.	4,013,000	3	3	25-28	
Microthecium retisporum Udagawa & Cain	7,000	1	1	21-24	
Mucor attenuatus Linn.	36,000	6	6	17-20	
Mucor hiemalis Wehmer	11,000	4	4	21-24	
Myrothecium	10,000	1	1	21-24	
Myrothecium cinctum (Corda) Sacc.	16,000	2	2	25-28	
Oidiodendron	64,000	6	7	9-12	
Oidiodendron tenuissimum (Peck) Hughes	52,000	48	58	25-28	21 (19)
Oidiodendron truncatum Barron	21,000	5	5	9-12	

Organism	Mean no. of propagules /g soil	No. of soil samples	No. of isolates in collection	Observed optimum temperature range* (°C)	Calculated optimum temperature (°C)
Pachybasium niveum Rostr.	103,000	74	87	17-20	22 (19)
Paecilomyces	70,000	22	23	9-12	16 (15)
Paecilomyces carneus (Duché & Heim) Brown & Smith	60,000	55	72	21-24	19 (18)
Paecilomyces elegans (Corda) Mason & Hughes	6,000	3	3	9-12	
Paecilomyces marquandi (Massee) Hughes	37,000	74	91	17-20	19 (18)
Paecilomyces striatisporus Onions & Barron	8,000	5	5	21-24	
Penicillium (11)	107,000	54	67	13-16	19 (18)
Penicillium (12)	55,000	11	13	21-24	
Penicillium (13)	91,000	24	37	17-20	18
Penicillium (14)	96,000	2	2	21-24	
Penicillium (15)	14,000	1	1	13-16	
Penicillium (16)	40,000	7	7	13-16	
Penicillium (17)	60,000	5	5	17-20	
Penicillium (18)	55,000	6	7	21-24	
Penicillium (19)	54,000	11	12	9-12	
Penicillium (20)	40,000	2	2	13-16	
Penicillium (21)	35,000	3	5	13-16	
Penicillium (22)	117,000	3	3	17-20	
Penicillium (23)	12,000	1	1	25-28	
Penicillium (24)	40,000	5	6	13-16	
Penicillium (26)	376,000	4	5	13-16	
Penicillium (27)	42,000	5	5	9-12	
Penicillium (28)	55,000	3	3	9-12	
Penicillium (30)	36,000	4	4	21-24	
Penicillium (33)	394,000	4	5	9-12	
Penicillium (34)	32,000	3	3	21-24	
Penicillium (36)	20,000	1	1	17-20	
Penicillium (38)	10,000	1	1	21-24	
Penicillium (39)	73,000	7	9	9-12	
Penicillium (40)	21,000	1	1	9-12	
Penicillium (41)	78,000	7	8	13-16	
Penicillium (42)	21,000	1	1	9-12	
Penicillium (46)	67,000	3	4	21-24	
Penicillium (47)	142,000	2	2	17-20	
Penicillium (48)	24,000	1	2	13-16	
Penicillium (50)	39,000	5	5	13-16	

Organism	Mean no. of propagules /g soil	No. of soil samples	No. of isolates in collection	Observed optimum temperature range* (°C)	Calculated optimum temperature (°C)
Penicillium (52)	38,000	1	1	9-12	
Penicillium (55)	20,000	1	1	17-20	
Penicillium (56)	81,000	1	1	9-12	
Penicillium (57)	6,000	1	1	13-16	
Penicillium (59)	110,000	1	1	21-24	
Penicillium (64)	44,000	3	3	13-16	
Penicillium (66)	10,000	1	1	21-24	
Penicillium (68)	71,000	1	1	13-16	
Penicillium (69)	10,000	1	1	21-24	
Penicillium (75)	16,000	6	7	21-24	
Penicillium (76)	680,000	1	1	25-28	
Penicillium (82)	5,000	1	1	21-24	
Penicillium (87)	37,000	1	1	25-28	
Penicillium (94)	103,000	3	3	21-24	
Penicillium (95)	58,000	1	1	21-24	
Penicillium (96)	114,000	2	2	21-24	
Penicillium (100)	22,000	1	1	21-24	
Penicillium (711)	200,000	1	1	13-16	
Penicillium (720)	11,000	1	1	21-24	
Penicillium (726)	51,000	1	1	21-24	
Penicillium (810)	14,000	1	1	17-20	
Penicillium (814)	2,000	1	1	17-20	
Penicillium (817)	76,000	1	1	21-24	
Penicillium (820)	113,000	3	4	21-24	
Penicillium (823)	14,000	1	1	17-20	
Penicillium (825)	40,000	1	1	17-20	
Penicillium brefeldianum Dodge	22,000	1	1	17-20	
Penicillium lanosum Westling	131,000	2	2	13-16	
Penicillium notatum Westling	13,000	1	1	17-20	
Penicillium steckii Zaleski	27,000	6	7	21-24	
Penicillium waksmani Zaleski	4,000	2	2	13-16	
Pestalozzia	12,000	1	1	17-20	
Phialocephala	25,000	10	10	17-20	
Phialophora	10,000	1	1	17-20	
Phoma (531)	16,000	1	1	17-20	

Organism	Mean no. of propagules /g soil	No. of soil samples	No. of isolates in collection	Observed optimum temperature range* (°C)	Calculated optimum temperature (°C)
Phoma (532)	1,000,000	1	1	21-24	
Phoma (533)	20,000	1	1	13-16	
Pseudeurotium zonatum van Beyma	7,000	1	1	17-20	
Pyrenochaeta	105,000	4	4	9-12	
Thysanophora penicillioides (Roum.) Kendrick	15,000	1	1	25-28	
Trichocladium opacum (Corda) Hughes	25,000	1	1	9-12	
Trichoderma (170)	39,000	183	238	17-20	19 (18)
Trichoderma (192)	34,000	5	5	21-24	
Trichoderma (193)	22,000	1	1	13-16	
Trichoderma hamatum (Bonn.) Bain (178)	42,000	112	151	13-16	18 (17)
Trichoderma hamatum (179)	62,000	1	1	21-24	
Trichoderma harzianum Rifai (174)	39,000	4	4	21-24	
Trichoderma harzianum (198)	1,000	1	1	25-28	
Trichoderma harzianum (199)	13,000	1	1	21-24	
Trichoderma koningii Oud.	75,000	89	121	21-24	20 (19)
Trichoderma polysporum (Link ex Pers.) Rifai	7,000	1	1	21-24	
Trichoderma viride Pers ex S.F. Gray	14,000	5	6	17-20	
Volutella	19,000	1	1	25-28	
Zygorhynchus moelleri Vuillemin	30,000	135	148	25-28	21 (19)
Unknown (450)	44,000	1	2	21-24	
Unknown (571)	241,000	59	68	17-20	20 (19)
Unknown (851)	21,000	1	1	25-28	
Unknown (861)	16,000	1	1	17-20	

*The temperature range and the calculated optimum temperatures are those taken 1 cm below the surface. Temperatures in parentheses are similar calculations for measurements made 5 cm below the surface.

†The identity of these isolates is not certain.

propagules g^{-1} isolated from different geographical locations of the pastures supported by forest soils were detected in the seasons 1967 to 1969 (Brewer et al. 1971) and the results in Table I show that the same conclusion is valid for the 1973 to 1975 seasons. The mean value for all the results given in Table I is 8.2×10^5 and the standard deviation of the 10 means is 2.9×10^5 (omitting the value 1.3×10^7 from the calculations).

A list of the 142 classified fungi that have been isolated from soil samples collected between 1967 and 1975 is given in Table II. Of these fungi, 137 have been assigned to a genus and 54 to species. Of these 54, one, *Aspergillus chevalieri* var *intermedius* (Taxonomic code 111) , is a distinct variety, the 2 strains of *Trichoderma hamatum* are clearly separable, as are the 3 of *Trichoderma harzianum* and the 2 of *Alternaria alternata.* It is possible that those isolates now classified with respect to genus only (e.g., *Circinella*) are a group of several different species, and contrariwise, those now separated as numbered isolates within a genus, (e.g., *Penicillium* 34, 36) will prove to be the same species. Isolates of these 142 fungi constitute 35% of all the isolates in the collection. The total number of propagules cultivated from all soil samples was $6.9 \times 10^5 \times 437 = 3.02 \times 10^8$. The number of propagules in the list of fungi in Table II is 1.15×10^8, or 38% of the total. In Table II the number of isolates of each organism in the collection is given and the number of soil samples from which each was isolated. The most common organism, *Zygorhynchus moelleri*, was found in 135 soil samples, or about 30% of those collected. The mean number of propagules g^{-1} soil of classified organisms is given in Table II. There are only 23 organisms in Table II that have been isolated from 10 or more soil samples, thus the frequencies given in the other cases are uncertain. Only 3 organisms—*Penicillium* sp. 11, *Pachybasium niveum* and the unknown species 571—have been found in numbers greater than 10^5 in more than 20 soil samples.

In the 9-year period, soil samples were collected when the soil temperature lay in the range 0-28°C. When the number of soil samples collected in the 4-degree temperature ranges 0-4°C, 5-8°C, etc. were calculated, the results fitted the equation:

$$\textit{numbers of collections} = -7.12 + 5.33x - 0.17x^2$$

where x is the maximum of the soil temperature range, with an index of fit of 0.9. Such a curve has a maximum at 16°C and variations from this maximum might be a characteristic of a particular species. The numbers of propagules of each of the fungi in Table II collected in soil temperature ranges of 4 degrees, between 0°C and 32°C at collection time was therefore calculated, and the range in which the maximum numbers were found at 1 cm depth is given. Where organisms occurred in more than 20 soil samples and at least 5 temperature ranges, the data were used to calculate a least mean squares fit to an equation of the second degree. The maximum value for temperature in the calculated relationship was then found by differentiation, in the usual way. The result gives the apparent optimum temperature for growth in the field for a particular species. This temperature is given in appropriate cases in Table II. The results of similar calculations are also given for soil temperatures measured 5 cm below the surface. The results in the majority of cases are greater than 16°C and in the instance of *Pachybasium niveum* the optimum temperature for isolation is apparently 22°C.

In 1974 and 1975 an attempt was made to obtain information about some aspects of the physiology of the soil isolates. This was done by incorporating the polysaccharides starch and cellulose in the medium, the hydrolysis of these polymers could be detected directly on the isolation plates. Similarly, reduction by a colony of the antibacterial dyestuff rose bengal, normally incorporated into the medium, could be easily detected. Finally, inhibition by a colony of another colony was readily seen. These 4 tests provide a simple assessment of some aspects of the physiology of the flora, and in practice proved so successful that they were retrospectively applied to such viable isolates as were in the collection for the years 1969, 1971, and 1973. Two hundred and three soil samples were collected in this period on 98 different occasions, and from these samples, 2683 isolates were obtained in culture. The mean value for the frequency (propagules g^{-1}) for each collection date was calculated and the results obtained, sorted as before into intervals of 10^5 g^{-1}. The resulting histogram is drawn in Figure 2. Its similarity to the corresponding histogram for the whole experimental period is clear. The mean value for the 98 collection dates was 8.1×10^5 propagules g^{-1} and a linear least means squares fit of the data gave a line with gradient 81; the calculated value for the first day (April 22 1969) was 7×10^5, and for the last day (October 28 1975), 8.7×10^5. Though this difference is greater than the difference calculated for the period 1967 to 1975, it is obviously insignificant. None of the classified isolates collected in this group were observed to hydrolyze cellulose. Such isolates that hydrolyzed starch, reduced rose bengal and inhibited the growth of other fungal colonies are found in a list in Table III. The mean values given in Table III are number of propagules of the species having the designated activity, that were found in 1 g of soil. The number of soil samples from which such species were isolated is also given in Table III. Of the 17 most common species (Table II), only one—*Absidia glauca*—is absent from Table III. The activity of certain species is striking; thus 20% of *Penicillium* sp. 11 hydrolyzed starch, and 6% inhibited the growth of other fungi. Ten percent of all *Trichoderma* species reduced rose bengal and 6% inhibited the growth of other fungal colonies. Isolates of two very common species—*Gliocladium roseum* and *Paecilomyces marquandi*—were active in all 3 tests.

Information on the physiological activity of unidentified isolates was also obtained, but it is not possible to present these data in a way that permits them to be related to a soil unit. The number of isolates that have not been classified in the 1969 and 1971 to 1975 periods is 1512, or 56%. One of these isolates hydrolyzed cellulose and 114 (4%) hydrolyzed starch. Rose bengal reduction was observed around colonies of 21 of these unclassified isolates and 45 (2%) inhibited the growth of other fungi. Activity in one or more of the 4 tests was observed in 11% of the isolates, classified and unclassified.

From the foregoing description of the soil fungal flora, a number of characters to which a numerical value can be assigned emerge. These numerical values allow comparisons to be made of the soil floras from two or more geographical locations. They can also be used to test how closely a sample of the flora corresponds to the whole. Here only the latter utility is discussed.

Selection of Random Samples from a Collection of Soil Fungi

A random sample of the estimated 3×10^8 propagules collected in this work was obtained by the use of dilution series (Montegut 1960). This random sample was then distorted by placing only 1 isolate of several colonies of the same organism found at a particular 10-fold dilution, in the culture collection. This distortion can be rectified by construction of a theoretical collection by multiple entry of each isolate in the real collection, the multiplication factor being a function of the isolate frequency. There are 2 extremes of this multiplication factor—a maximum case where the frequencies are divided by 1 giving an expanded collection of 3×10^8, and a minimum where the frequencies are divided by themselves to give 2683 cultures. In both cases the numbers are large enough to deter an examination of all. It is clear

Table III. Physiological properties of species of fungi isolated from soils of permanent pasture at Nappan, Nova Scotia.

	Starch hydrolysis		Rose bengal reduction		Antifungal activity	
Organism (code no.)	Mean*	No. of samples	Mean*	No. of samples	Mean*	No. of samples
Alternaria alternata (461)	7,400	1	0	0	0	0
Aspergillus chevaliere	4,800	1	0	0	0	0
Aspergillus fumigatus	0	0	0	0	9600	1
Aspergillus sydowi	0	0	0	0	36,000	1
Cladosporium cladosporioides	160,000	1	0	0	0	0
Fusarium (270)	32,000	3	0	0	8300	1
Fusarium oxysporum	0	0	0	0	19,000	1
Fusarium solani	16,000	1	0	0	0	0
Gliocladium atrum	13,000	1	0	0	0	0
Gliocladium roseum	13,000	1	21,300	3	41,500	2
Gongronella butleri	6350	2	0	0	0	0
Gymnoascus roseus	12,000	1	0	0	0	0
Myrothecium cinctum	13,000	1	0	0	0	0
Oidiodendron tenuissimum	50,400	11	0	0	0	0
Pachybasium niveum	20,000	1	0	0	130,000	1
Paecilomyces (180)	10,000	1	0	0	160,000	1
Paecilomyces marquandi	24,000	4	5100	1	45,500	2
Paecilomyces carneus	27,500	4	0	0	64,000	1
Penicillium (11)	168,000	11	0	0	41,000	3
Penicillium (12)	0	0	0	0	4800	1
Penicillium (13)	29,000	2	0	0	0	0
Penicillium (16)	11,000	1	0	0	37,000	1
Penicillium (18)	23,300	2	0	0	0	0
Penicillium (19)	197,000	1	197,000	1	0	0
Penicillium (26)	730,000	1	0	0	0	0
Penicillium (27)	0	0	0	0	60,500	2
Penicillium (30)	23,000	1	0	0	0	0
Penicillium (33)	930,000	1	0	0	0	0
Penicillium (34)	79,000	1	0	0	0	0
Penicillium (46)	51,000	1	0	0	0	0
Penicillium (48)	0	0	0	0	4800	1
Penicillium (720)	11,000	1	0	0	0	0
Penicillium brefeldianum	0	0	0	0	22,000	1
Penicillium notatum	0	0	0	0	13,000	1
Phoma (533)	20,000	1	0	0	0	0
Trichoderma (170)	0	0	50,700	5	39,000	21
Trichoderma hamatum	0	0	15,000	5	0	0
Trichoderma harzianum	0	0	13,000	1	0	0
Trichoderma koningii	0	0	72,000	28	14,000	1
Zygorhynchus moelleri	0	0	7400	2	28,000	2
Unknown (431)	56,000	1	0	0	0	0
Unknown (571)	750,000	10	0	0	39,000	1

*Number of propagules capable of the given activity.

that a further selection of a random number of isolates is needed. There are 3 questions concerning the way this random number is obtained: (1) How many cultures selected at random should be made from the expanded collection? (2) By what frequency factor should the culture collection be expanded? (3) Which of an infinite number of random samples fulfilling the first 2 criteria should be used for study? The answer to the first question was dictated by the human resources available and was set at 750. The last 2 questions can be settled on the basis of criteria developed from the description of the flora.

Size of Expanded Collection

The culture collection from 1969, and 1971 to 1975 was converted into 4 expanded collections. The expansions were made by dividing the frequency of each isolate by itself, 2 x 10^4, 10^4, and 10^3, and using the quotients to determine the number of times the isolate was entered into the expanded collection. Two conditions were imposed on this process. One was that every isolate must be entered at least once, and the other condition, applied to the last 3 collections, was that the maximum number of entries of a single isolate was, respectively, 28, 55, and 550. The resulting 4 collections contained 2683, 8047, 14,950, and 132,396 isolates. Random samples of 750 different entries from each of these 4 collections were then made. Random samples from each of these expanded collections showed no significant differences in the variation of the mean frequencies of all soil samples collected in each month of the 5 seasons. The standard deviations of the monthly means was about 30% of the overall mean and thus similar to that calculated for the collection as a whole (12%). Some other characters of the random samples are given in Table IV. It is evident that only small changes occur in the random sample by a 50-fold increase in the size of the expanded collection from which they were selected. Three examples of random samples from one expanded collection (14,950 entries) are also given in Table IV. Similar variability was found in random samples from the other expanded collections. In one respect none of the random samples resemble the total collection. This dissimilarity is the proportion of species, or isolates of unknown genus that inhibit the growth of other fungi. The ratios of the number of species that hydrolyze starch, inhibit growth and reduce rose bengal is 3.6:2.4:1 and the same ratios for these activities in the unknown isolates is 5.4:2.1:1, but in the case of the random samples they are about 4:0.5:1 and 5:0.4:1. The data in Table IV also show that there are many species known to be in the flora that are not selected in the random samples. Despite these problems, the information in Table IV allows a choice to be made of the size to which the collection should be expanded before taking a random sample that reflects the frequency of the isolates. Thus as the collection is expanded, the number of soil samples collected that are represented in the random sample decreases, and the gradient of the linear least mean squares fit of the frequency with respect to time increases. The number of different isolates selected, and hence the sample of the individuals in the flora, also decreases. Thus, expansion to 132,396 entries involves distortion of the flora in the random sample. The random sample taken from the smallest collection (2683) is, of course, unacceptable because no weighting has been given to those species that are predominant in the flora. It is interesting to note that the figures in Table IV also illustrate its unsuitability. Thus, the gradient of the linear least mean squares fit deviates from that of the total collection by the greatest magnitude of all the random samples given in Table IV. The ratio of the numbers of species that hydrolyze starch to those that inhibit other fungi is 13:1 in the random sample from the unexpanded collection, as compared to 3:2 for the collection as a whole. The choice between the expanded collections of 8047 and 14,950 entries was made on the basis of the greater similarity of the ratios

Table IV. Characteristics of random samples of isolates (750) selected from the culture collection, expanded by various factors related to frequency.

	Total collection	f	Random samples (750) of expanded collection Frequencies (f) divided by:				
			$2x10^4$	10^4			10^3
No. of collection days	98		96	96	97*	96	95
Gradient of linear least mean squares fit	81	-33	112	113*	124	118	144
No. of soil samples	193	193	189	185	191*	181	176
Geographical distribution; S.D. of % isolates selected for each sector		3.3	4.1	4.3	3.8	3.4*	3.9
No. of different isolates	2683	750	574	542*	526	538	513
Classified organisms							
Number	142	67	61	52	57*	54	62
No. > 20,000 g^{-1} from > 10 samples	21	20	19	19	20*	18	20
Biological activity. No. of classified organisms against:							
starch	29	13	12	10	12*	10	6
rose bengal	8	4	3	4*	3	2	3
fungi	19	1	0	2	3*	2	1
No. of unknown isolates active against:							
starch	114	36	26	28	25	26	21
cellulose	1	0	0	0	0	1	0
rose bengal	21	9	4	6	5	4	4
fungi	45	3	2	2	2	2	3

*Indicates score as discussed in the text.

of species active in the three biological tests to that of the total collection. The data given in Table IV for the collection expanded to 8047 are abnormal, as none of the species inhibited other fungi. The mean value for the ratio of starch hydrolysis to antifungal activity in 8 random samples was 11.5:1 and this is at greater variance with the ratio for the total collection than with that of the random samples (16) of the collection expanded to 14,950, which was 4.5:1. The reason for this odd result is not apparent to us, but it eased the choice of the latter expanded collection.

Choice of a Particular Random Sample for Study

The 3 sets of data given in Table IV for 3 random samples selected from the collection expanded to 14,950 entries show small differences. To enable a rational choice to be made between such samples a scoring system has been adopted where points are given to characters that are in closest accord with those of the total collection. The method is illustrated by reference to Table IV. One of the random samples contains isolates from one more collection date than the others and thus scores 1. The same sample also contains isolates from considerably more soil samples and thus scores another point. However, another sample has a linear least mean squares frequency-time fit that approximates more closely to that of the total collection and thus scores a point for this character, while the third random sample has a closer fit for the geographical distribution of its isolates for the different sectors. The scoring is indicated by asterisks in Table IV, and the sums of the scores for the 3 random samples are 2, 7 and 1. We have been surprised at the differences thus revealed and at how easily a choice could be made in this way. In addition to such objective criteria, it is desirable to look at random samples from the point of view of biological and/or chemical interest. For example, a choice between 2 random samples that scored very evenly by the method described might be made if one sample contained isolates having unusual properties e.g. the ability to hydrolyze cellulose, or unusual species, or species showing antifungal activity that have not been reported in the literature to produce such metabolites.

Quantitative Description of a Random Sample of 750 Fungal Isolates

The random sample of 750 isolates chosen for study, represented 182 soil samples collected on 96 collection dates. The gradient of the linear least mean squares fit of time against mean propagules $g^{-1}d^{-1}$ was 109, and the standard deviation of the percentage of isolates selected from each sector was 2.9. The number of different isolates selected was 543 and the ratios of the species that hydrolyzed starch, reduced rose bengal and inhibited other fungi were 9:3:2. One isolate of *Pachybasium niveum* inhibited the growth of *Zygorhynchus moelleri*. Of the isolates that have not so far been classified, 22 produced enzymes that hydrolyzed starch, 1 hydrolyzed cellulose, 3 reduced rose bengal, 1 isolate of *Penicillium* sp. 27 inhibited the growth of several fungal isolates and another unknown isolate inhibited the growth of a *Penicillium* sp. Sixty-one of the 750 samples (8%) were not viable at the time of assay (1978-1979); 40 of them (66%) were collected in 1969.

Sixty-seven species have been classified—the number is not comparable to those in Table IV because these isolates have been the object of closer scrutiny. This represents 49% of the total. They are given in Table V in the same format as Table II except that the number of isolates is the number in the random sample and therefore is greater than the number in the collection in a few cases. Of the 21 species in the total collection that have frequencies greater than 2×10^4 g^{-1} and occurred in more than 10 soil samples, 19 are found in this random sample. When the temperature range (4 degrees C) at which the greatest number of propagules were found was calculated for the species selected in the random sample it was found to

Table V. Fungi selected in the random sample used for growth inhibition studies, mean frequencies of selected species, number of soil samples from which they were isolated, and "optimum" temperatures for growth in soil.

Organism (Code No.)		Mean frequency (propagules g-1)	No. of soil samples	No. of isolates selected	Observed optimum temperature range (°C)	Calculated optimum temperature (°C)
Absidia glauca		40,000	2	3	17-20	
Alternaria alternata	(462)	14,000	1	1	17-20	
Cladosporium cladosporioides		230,000	2	3	21-24	
Cladosporium herbarum		29,000	4	4	21-24	
Cunninghamella elegans		71,000	1	1	25-28	
Cylindrocarpon destructans		16,000	1	1	17-20	
Fusarium	(270)	32,000	2	2	13-16	
Fusarium avenaceum		31,000	1	1	17-20	
Fusarium solani		29,000	1	1	17-20	
Gliocladium atrum		44,000	1	1	13-16	
Gliocladium deliquescens		24,000	1	1	29-32	
Gliocladium roseum		116,000	17	25	13-16	18
Gongronella butleri		239,000	15	24	13-16	18
Metarrhizium anisopliae		6,017,000	2	3	25-28	
Oidiodendron tenuissimum		86,000	10	12	9-12	
Pachybasium niveum		152,000	10	14	9-12	18
Paecilomyces carneus		90,000	12	16	21-24	20
Paecilomyces marquandi		43,000	9	11	21-24	20
Penicillium	(11)	127,000	6	9	21-24	
Penicillium	(12)	135,000	2	2	25-28	
Penicillium	(13)	128,000	5	7	17-20	
Penicillium	(14)	170,000	1	1	21-24	
Penicillium	(16)	130,000	1	1	13-16	
Penicillium	(17)	180,000	1	1	17-20	
Penicillium	(18)	110,000	1	1	21-24	
Penicillium	(19)	74,000	4	6	9-12	
Penicillium	(20)	19,000	1	1	9-12	
Penicillium	(22)	164,000	2	4	17-20	
Penicillium	(24)	51,000	3	5	13-16	
Penicillium	(26)	483,000	3	7	13-16	
Penicillium	(27)	36,000	2	2	13-16	

Penicillium	(28)	100,000	1	3	9-12	
Penicillium	(33)	730,000	2	4	9-12	
Penicillium	(34)	79,000	1	1	21-24	
Penicillium	(36)	20,000	1	1	17-20	
Penicillium	(39)	110,000	4	5	9-12	
Penicillium	(41)	230,000	1	1	13-16	
Penicillium	(42)	21,000	1	1	9-12	
Penicillium	(46)	63,000	2	2	21-24	
Penicillium	(52)	38,000	1	2	9-12	
Penicillium	(56)	81,000	1	1	9-12	
Penicillium	(64)	43,000	1	1	25-28	
Penicillium	(66)	10,000	1	1	21-24	
Penicillium	(68)	71,000	1	1	13-16	
Penicillium	(75)	32,000	1	1	25-28	
Penicillium	(76)	680,000	1	3	25-38	
Penicillium	(94)	290,000	1	1	21-24	
Penicillium	(96)	114,000	2	3	21-24	
Penicillium	(711)	200,000	1	2	13-16	
Penicillium	(720)	11,000	1	1	21-24	
Penicillium	(726)	51,000	1	1	21-24	
Penicillium	(820)	165,000	2	5	21-24	
Penicillium	(825)	40,000	1	2	17-20	
Penicillium steckii		20,000	1	1	21-24	
Phoma	(532)	1,000,000	1	5	21-24	
Phoma	(533)	20,000	1	1	13-16	
Pseudeurotium zonatum		7,000	1	1	17-20	
Pyrenochaeta	(540)	34,000	1	1	9-12	
Trichoderma	(170)	32,000	3	3	17-20	
Trichoderma	(192)	76,000	1	1	21-24	
Trichoderma hamatum	(178)	84,000	26	38	13-16	18
Trichoderma harzianum	(174)	71,000	2	2	21-24	
Trichoderma koningii		169,000	25	46	21-24	19
Volutella	(701)	19,000	1	1	25-28	
Zygorhynchus moelleri		40,000	10	11	9-12	14
Unknown	(571)	03,000	19	38	17-20	20

be the same in 76% of the species as was calculated for the collection as a whole. Only two species—*Pachybasium niveum* [22°C (collection), 18°C (random sample)] and *Zygorhynchus moellerii* (21°C, 14°C)—differed greatly in the calculated optimum growth temperatures for the collection as a whole and for the random sample. The biological activity of the different species in this random sample is given in Table VI. Of the 750 isolates selected, 182 inhibited the growth of *S. lutea*, 24 in the growth of *C. utilis* and 22 the growth of both test organisms. Thus

Table VI. Metabolic and growth-inhibiting activity of fungal species randomly selected from an expanded culture collection of 14,950 isolates cultivated from soil of permanent pasture.

		Metabolic activity (propagules g^{-1} soil)									
		Starch hydrolysis		Rose bengal reduction		Growth inhibition					
						Antifungal activity		*S. lutea*		*C. utilis*	
Organism (Code no.)			No.*		No.*		No.*		No.*		No.*
Fusarium	(270)	0	0	0	0	0	0	32,000	2	22,000	1
Fusarium solani		0	0	0	0	0	0	29,000	1	0	0
Gliocladium atrum		0	0	0	0	0	0	44,000	1	0	0
Gliocladium roseum		0	0	0	0	0	0	112,940	15	36,000	1
Gongronella butleri		0	0	0	0	0	0	0	0	14,000	1
Metarrhizium anisopliae		0	0	0	0	0	0	6,017,000	2	0	0
Oidiodendron tenuissimum		95,500	2	0	0	0	0	0	0	29,000	1
Pachybasium niveum		0	0	0	0	130,000	1	124,750	4	200,000	1
Paecilomyces marquandi		0	0	0	0	0	0	18,600	2	0	0
Paecilomyces carneus		0	0	0	0	0	0	30,400	2	60,200	5
Penicillium	(11)	63,000	1	0	0	0	0	12,000	1	0	0
Penicillium	(12)	0	0	0	0	0	0	110,000	1	0	0
Penicillium	(13)	0	0	0	0	0	0	83,600	5	0	0
Penicillium	(19)	130,000	1	130,000	1	0	0	130,000	1	0	0
Penicillium	(20)	0	0	0	0	0	0	19,000	1	0	0
Penicillium	(24)	0	0	0	0	0	0	40,000	1	0	0
Penicillium	(26)	730,000	1	0	0	0	0	483,000	3	0	0
Penicillium	(27)	0	0	0	0	11,000	1	36,000	2	0	0
Penicillium	(33)	930,000	1	0	0	0	0	730,000	2	0	0
Penicillium	(34)	79,000	1	0	0	0	0	79,000	1	79,000	1
Penicillium	(39)	0	0	0	0	0	0	40,000	2	0	0
Penicillium	(41)	0	0	0	0	0	0	230,000	1	0	0
Penicillium	(46)	0	0	0	0	0	0	100,000	1	0	0
Penicillium	(56)	0	0	0	0	0	0	81,000	1	0	0
Penicillium	(76)	0	0	0	0	0	0	680,000	1	0	0
Penicillium	(720)	11,000	1	1	0	0	0	0	0	0	0
Penicillium	(825)	0	0	0	0	0	0	40,000	1	0	0
Phoma	(533)	20,000	1	0	0	0	0	0	0	0	0
Pseudeurotium zonatum		0	0	0	0	0	0	7,000	1	0	0
Pyrenochaeta	(540)	0	0	0	0	0	0	34,000	1	0	0
Trichoderma	(170)	0	0	0	0	0	0	46,000	1	0	0
Trichoderma hamatum	(178)	0	0	3,400	1	0	0	44,200	15	50,800	3
Trichoderma koningii		0	0	171,000	9	0	0	252,000	10	0	0
Volutella	(701)	0	0	0	0	0	0	19,000	1	0	0
Unknown	(571)	1,660,000	4	0	0	0	0	0	0	0	0

*Number of isolates in random sample.

growth-inhibitory activity was found in about 30% of the cultures selected for the random sample. The proportion is probably somewhat bigger if the fact that 8% of the selected cultures were not viable and could not be tested, is taken into account.

An examination of Tables V and VI reveals that 91% of isolates of *Gliocladium roseum*, 40% of isolates of *Trichoderma koningii*, and 58% of isolates of *T. hamatum* produce growth-inhibiting metabolites in culture. Isolates having this ability were found in 16%, 11%, and 16%, respectively, of all the soil samples collected. In Table II it is shown that the 3 species rank sixth (6.6×10^6), fifth (6.7×10^6) and ninth (4.7×10^6) in the numbers of fungal propagules of particular species collected in the experimental period 1967 to 1975. The species that is next in ability to produce growth-inhibiting metabolites is *Paecilomyces carneus*, found in 7% of the soil samples collected, ranked eleventh (3.3×10^6) in Table II, and 58% of whose isolates (7 out of 12) were active. Similar calculations in the cases of other species reveal a large decrease in the probability that a soil sample will provide an isolate in culture that will produce a growth-inhibiting metabolite.

Of the 383 (278 different) isolates in the random sample of 750 that are unclassified at present, 86 (60 different) inhibited the growth of *S. lutea* and 26 (22) the growth of *C. utilis*. The growth of both test organisms was inhibited by 13 isolates (10 different).

Discussion

In Figure 2, 763 determinations of the number of propagules g^{-1} are recorded. Some of the data are incorporated into both histograms, so the histograms cannot simply be added. Nevertheless, this large body of data seems to support the argument that the number of propagules g^{-1} follows a probability distribution with a maximum. It is noteworthy that this maximum remains the same (Fig 2) when the mean number of propagules g^{-1} collected on a particular day is used as the measure of soil fungal density even though the mean number of propagules g^{-1} in the latter case is 15% greater. The stability of the flora over the period of 9 years is remarkable and is in accord with the conclusions of Brewer et al. (1971) concerning the stability of fungal floras in forest-derived and marshland-derived soils. Much work remains to be done on the classification of isolates, especially the *Penicillia* isolated in 1974 and 1975 — many of those classified as unknown in the random sample belong to this genus. Despite this ignorance we have the impression that certain species, e.g. *Chaetomium cochliodes*, *Fusarium poae*, and *F. avenaceum*, are less common among the 1975 isolates than they were among those collected in 1967. It is clear that much information concerning the behaviour of individual species during the period of our studies will come to light when the detailed taxonomic work is completed. We hope to report work on individual species when it is to hand.

The results in Table II are an attempt to assess the flora of these pasture soils quantitatively. Thus 2 species, *Gongronella butleri* and the unknown fungus 571, account for 8% of all the fungal propagules isolated. This assessment of the importance of different species could be mechanically applied to all those in the list, but is of doubtful value in the case of those species that have been found in less than 10 to 20 soil samples. However, it is clear that relatively few species constitute a major portion of the soil fungal flora of these pastures, and since the majority (90%) of these predominant species were found in the random sample used to determine the ability of the flora to produce growth inhibiting metabolites, the results might be justifiably extrapolated to the flora as a whole.

We consider the results given in Tables V and VI remarkable. The 3 species — *Gliocladium roseum, Trichoderma koningii*, and *T. hamatum* collectively constitute about 6% of all the fungal propagules isolated from 437 g soil and from the biological assay results it can be calculated that about 4% of the propagules isolated consist of these 3 species that have the ability to hinder the growth of other organisms. On the basis of our earlier qualitative work (Brewer et al. 1972), we concluded that *Trichoderma* spp. were an important part of the soil fungal flora, capable of producing metabolites that were inhibitory to growth. This work is therefore in agreement and, further, places the evidence on a more quantitative basis. It has been shown that some of the toxic metabolites of *Trichoderma hamatum* affect rumen fermentation (Brewer et al. 1979; Jones and Jen unpubl.) thus augmenting the circumstantial evidence that links this genus with the ill-thrift of young sheep and cattle that graze these pastures (Brewer et al. 1971).

On a wider scene it seems possible that the techniques we have used in our attempt to get quantitative information about the fungal flora of pasture soils, will have applicability to other ecological niches. One immediately thinks of the aerial fungal flora which changes more rapidly than its soil counterpart, but other situations such as distributions of microscopic aquatic plants and animals or even lichens in a prescribed area, may well benefit from similar analysis.

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Appendices

A. Program used to write files of data describing fungal isolates from soil.

```
01000 FILE#1="A1",#2="OLDFIL",
01005#3 = "NEWFIL"
01010 ON ERROR THEN 9040
01020 RESTORE #2
01030 FOR X=1 TO 2000
01040 READ D,M,Y,P,S,I,T,T1,N,D1,S1
01050 READ T2,S2,S3,A,C,R1,R
```

Each time the program is run the data are written on the temporary file "A1" in correct format. This file is then added to existing information residing on "Oldfil" to create "Newfil". Each experimental result is read from right to left as it appears in the field book (lines 1040 and 1050).

```
01060 R=R*25.4
01070 R=INT (R+.5)
01080 S2=(S2-S3)/2
01090 S2=INT (S2+.5)
01100 IF S2<10 THEN 1120
01110 S2=9
01120 N=(N*10**D1)/S1
01130 FOR Z=0 TO 9
01140 IF INT (N/10**Z)>10 THEN 1160
01150 GOTO 1170
01160 NEXT Z
01170 N=(N/(10**(Z-1)))+.5
01180 N=INT (N)
01190 N=(N*10)+Z
01200 T=INT(T+.5)
01210 T1=INT(T1+.5)
```

Lines 1060 to 1210 calculate values that appear on the file from those read on lines 1040 and 1050; e.g. rainfall is converted from inches to an integral number of millimeters by lines 1060 and 1070. The frequency (propagules g^{-1}) is calculated on line 1120 and its value converted to the format described in the text by lines 1130 to 1190.

```
01220 D=(D*10**4)+(M*1000)+(Y*100)+P
01230 S=(S*10**5)+(I*1000)+N
01240 A=(A*10**7)+(C*10**6)+(R1*10**5)
01250 A=A+(S2*10**4)+T2
01260 T=(T*10**4)+(T1*100)+R
```

Lines 1220 to 1260 put the data into the correct format.

```
01270 WRITE #1,D,S,A,T
```

Each line of code is written onto the scratch file "A1".

```
01280 NODATA 1300
01290 NEXT X
01300 PRINT "NUMBER OF CULTURES";
01305 PRINT "WRITTEN";
01310 PRINT " ON SCRATCH FILE ";X
01320 PRINT " "
01330 NODATA #2,1390
```

The x loop continues to cycle (lines 1030 to 1290) until all the field book data are read.

```
01340 FOR X1=1 TO 20000
01350 READ #2,D,S,A,T
01360 WRITE#3,D,S,A,T
01370 NODATA # 2,1390
01380 NEXT X1
```

The x1 loop starts to write the updated file "Newfil", beginning with the data already in the computer system. Line 1330 serves to bypass this section if such data do not exist.

```
01390 RESTORE#1
01400 FOR X2=1 TO X
01410 READ#1,D,S,A,T
01420 WRITE#3,D,S,A,T
01430 NEXT X2
01440 RESTORE#3
01450 PRINT "FIRST 3 LINES ON NEW FILE"
01460 PRINT " "
```

The new data are added to the old data by the loop x2.

```
01470 FOR X3=1 TO 30000
01480 READ#3,D,S,A,T
01490 IF X3>3 THEN 1560
01500 PRINT D,S,A,T,
01510 IF X3 <>3 THEN 1580
01520 PRINT " "
01530 PRINT "LAST 3 LINES ON NEW FILE"
01540 PRINT " "
01550 GOTO 1580
01560 IF X3<X+X1-2 THEN 1580
01570 PRINT D,S,A,T
01580 NODATA # 3,1600
01590 NEXT X3
01600 PRINT " "
01610 PRINT "NUMBER OF CULTURES";
```

The loop X3 is provided so that the mycologist knows that:

(a) The correct number of cultures has been written on the new file.
(b) The total number of isolates on the new file is correct.
(c) The first 3 lines and the last 3 lines on the new file are given so that these can be checked with the record in the field book.

```
01620 PRINT " ON NEW FILE ";X3
01630 STOP
09040 RESTORE #1
09050 PRINT "NUMBER OF CULTURES";
09055 PRINT "WRITTEN";
09060 PRINT " ON FILE BEFORE CRASH";X
09070 PRINT " "
09080 FOR X4=1 TO X
09090 READ#1,D,S,A,T
09100 IF X4>3 THEN 9180
09110 PRINT D,S,A,T
09120 IF X4<>3 THEN 9200
09130 PRINT " "
09140 PRINT " "
09150 PRINT "LAST 3 LINES WRITTEN"
09160 PRINT " "
09170 GOTO 9200
09180 IF X4<X-2 THEN 9200
09190 PRINT D,S,A,T
09200 NODATA #1,9220
09210 NEXT X4
09220 END
```

The lines 9040 to 9220 give information if an error has occurred in the calculations. The following facts are given:

(a) The number of cultures written on the file before the error occurred.
(b) The first 3 lines on the file of new data (this indicates if the data were entered correctly).
(c) The last lines of data read. This is useful to trace the error.

Notes.
Before running the program, data are typed into it from the field book or transmitted from a tape cassette. Data should be in the format: 2000 data 23,6,4,3, . . etc. 18 entries on each line, each entry separated by a comma. Zeros are used when no observations exist. The program is then 'run'; the exact command differs slightly with different systems.

Finally the new file 'Newfil' must be renamed 'Oldfil', the old file discarded and the 'Newfil' saved.

B. Program for expanding fungal data files with respect to frequency, and selecting random samples therefrom.

```
01000 DATA 90,4,120,5,151,6,181,7,212,8
01010 DATA 243,9,273,0,304,1
01020 FILE #1="CULTFIL",#2="EXPCOL"
01030 FILE #3="RANDSEL",#4="ISOLATS"
01040 RESTORE #1
01050 DIM N(750), M(10,2),S(100,6)
```

The first 2 lines are a calendar, used to calculate the day number.

The file 'cultfil' is the file of fungal isolates from which the expanded file 'expcol' is created. The file 'randsel' is the random sample of 750 en-

```
01060 MAT M=ZER
01070 MAT S=ZER
01080 MAT N=ZER
01090 T=0
01100 FOR X=1 TO 26000
01110 READ#1,A,B,C,D
01120 Z=INT(A/100)*100
01130 Z1=INT(Z/10**4)
01140 Z2=INT(Z/1000)-(Z1*10)
01150 Z=INT(Z/100)-((Z1*100)+(Z2*10))
01160 IF Z=0 THEN 01420
01170 IF Z=7 THEN 01420
01180 IF Z=8 THEN 01420
01190 GOSUB 02510
01200 M(Z3,1)=M(Z3,1)+1
01210 RESTORE
01220 FOR X1=1 TO 8
01230 READ J,J1
01240 IF J1<>Z2 THEN 01270
01250 Z1=Z1+J
01260 GOTO 01280
01270 NEXT X1
01280 IF Z>6 THEN 01300
01290 Z=Z+10
01300 Z1 = (((Z-7)*365)+ Z1) - 113
01310 B1=INT(B/10)-(INT(B/1000)*100)
01320 B9=B-(INT(B/10)*10)
01330 B1=B1*(10**(B9-1))
01340 IF B1>6*10**5 THEN 01370
01350 B2=1+INT(B1/10**4)
01360 GOTO 01380
01370 B2=55
01380 FOR X2=1 TO B2
01390 WRITE#2,A,Z1,B,B1,C,D
01400 T=T+1
```

tries from 'expcol' and 'isolats' is a file of all the different isolates that have been written on 'randsel'.

The x-loop (lines 1100-1430) does the following jobs:

(a) It calculates the day number the propagule was isolated (lines 1210-1300).

(b) It calculates the frequency (propagules g^{-1}) (lines 1310-1330).

(c) It finds the sector from which the soil was collected and records in matrix m that an isolate was collected therefrom. (lines 1190 and 1200).

(d) It writes the expanded file 'expcol'; the number of multiple entries is calculated by lines 1350-1410.

```
01410 NEXT X2
01420 NODATA #1, 01440
01430 NEXT X
01440 RESTORE # 2
01450 Z=Z1=Z2=0
```

Lines 1460-1520 generate 750 random numbers—all different—lying between the values 1 and the number of entries on the expanded file ('expcol').

```
01460 FOR X3=1 TO 750
01470 Z=INT(1+T*RND(-1))
01480 FOR X4=1 TO X3-1
01490 IF Z=N(X4) THEN 01470
01500 NEXT X4
01510 N(X3)=Z
01520 NEXT X3
```

Lines 1530-1630 sort the 750 random numbers into *ascending* order.

```
01530 FOR X5=1 TO 750
01540 Z=2*T
01550 FOR X6=X5 TO 750
01560 IF Z < N(X6) THEN 01590
01570 Z=N(X6)
01580 Z1=X6
01590 NEXT X6
01600 Z2=N(X5)
01610 N(X5)=Z
01620 N(Z1)=Z2
01630 NEXT X5
01640 Z=Q=Q1=K=1
01650 T1=0
```

Lines 1660-1720 write the file of randomly selected isolates and in addition (for convenience) record the day number and frequency of each isolate. The selection is done by the value of the counter x7 which varies between 1 and the number of entries in the expanded collection ('expcol'). When the value of x7 = the value of a selected random number, the entry that has been read is written on the file 'randsel'.

```
01660 FOR X7=1 TO T
01670 READ # 2,A,Z1,B,B1,C,D
01680 IF Z=751 THEN 01730
01690 IF X7<>N(Z) THEN 01720
01700 WRITE #3,A,Z1,B,B1,C,D
01710 Z=Z+1
01720 NEXT X7
01730 RESTORE #3
01740 FOR Y=1 TO 750
01750 READ #3,A,Z1,B,B1,C,D
```

```
01760 IF A<> Q THEN 01790
01770 IF B<> Q1 THEN 01790
01780 GOTO 01990
01790 GOSUB 02510
01800 M(Z3,2)=M(Z3,2)+1
01810 FOR X8=1 TO K
01820 IF S(X8,1)=Z1 THEN 01880
01830 IF S(X8,1)<>0 THEN 01870
01840 S(X8,1)=Z1
01850 K=K+1
01860 GOTO 01880
01870 NEXT X8
01880 S(X8,2)=S(X8,2)+B1
01890 FOR X9=3 TO 6
01900 IF S(X8,X9)=Z3 THEN 01950
01910 IF S(X8,X9)<>0 THEN 01940
01920 S(X8,X9)=Z3
01930 GOTO 01950
01940 NEXT X9
01950 Q=A
01960 Q1=B
01970 WRITE #4,A,B,C,D
01980 T1=T1+1
01990 NEXT Y
02000 FOR X0=1 TO K-1
02010 FOR X=1 TO 4
02020 IF S(XO,X+2)=0 THEN 02040
02030 NEXT X
02040 S(XO,2)=S(XO,2)/(X-1)
02050 NEXT XO
02060 K=K-1
02070 Q=Q1=Q2=Z=0
02080 FOR X1=1 TO K
02090 Q=Q+S(X1,1)
```

The y-loop—lines 1740-1990—does the following jobs:

(a) It writes a new file 'isolats' where all replicate entries on 'randsel' are rejected, i.e. all entries on 'isolats' are unique.

(b) It calculates the sector from which the soil was collected and records that an isolate from that sector was selected, accumulating the sum.

(c) It sums all the frequencies collected on each collection day and remembers how many soil samples were collected on that day.

(d) It sums all soil samples collected (k).

(e) It adds all the different isolates (t).

The x0 loop calculates the mean propagules g^{-1} for each day of collection.

At this point in the program (after line 2030) the file 'isolats' can be printed out, by inserting a suitable loop. This is useful as a temporary notebook for recording further results acquired by subsequent study of the random sample.

```
02100 Q1=Q1+S(X1,2)
02110 Q2=Q2+(S(X1,1)**2
02120 Z=Z+(S(X1,1)*S(X1,2))
02130 NEXT X1
02140 Z7=((K*Z) - (D*Q1))/((K*Q2) - (Q*Q))
02150 Z8=(Q1/K) - (Z7*(Q/K))
02160 PRINT "COEFFICIENTS OF LINEAR";
02170 PRINT "LEAST MEANS SQUARES FIT";
02180 PRINT Z8,Z7
02190 PRINT "NUMBER OF COLLECTION";
02195 PRINT "DATES";
02200 PRINT "SELECTED";K
02210 PRINT " "
02220 PRINT "NUMBER OF DIFFERENT"
02230 PRINT "ISOLATES SELECTED"; T1
02240 PRINT " "
02250 PRINT "GEOGRAPHICAL DISTRIBUTION";
02260 PRINT "OF ISOLATES"
02270 PRINT " "
02280 PRINT "SECTOR";TAB(12);"NO. OF";
02290 PRINT TAB(22); "PERCENT"
02300 PRINT TAB(12)"ISOLATES";TAB(22);
02310 PRINT "OF TOTAL"
02320 PRINT " "
02330 S=T=0
02340 FOR X2=1 TO 10
02350 PRINT TAB(4);X2;TAB(11);M(X2,1);
02360 P=M(X2,2)*100/M(X2,1)
02370 PRINT TAB(16);M(X2,2);TAB(23);
02380 PRINT INT(P+.5)
02390 S=S+P
02400 NEXT X2
02410 S=S/10
```

The remainder of the program is arithmtic. A linear least mean squares fit of the data (day number:mean frequency) is calculated in the usual way by the lines 2080-2150.

```
02420 FOR X3=1 TO 10
02430 P=M(X3,2)*100/M(X3,1)
```

Lines 2420-2470 calculate the standard deviation of the % isolates of the total collected from each sector.

```
02440 T=T+((P-S)**2)
02450 NEXT X3
02460 T=T/9
02470 T=SQR(T)
02480 PRINT "STANDARD DEVIATION OF":
02490 PRINT"% DISTRIBUTION";T
02500 STOP
02510 Z3=INT(B/10**5)
02520 IF Z3=0 THEN 02550
02530 IF Z3>10 THEN 02570
02540 GOTO 02580
02550 Z3=10
02560 GOTO 02580
02570 Z3=INT(1+10*RND(-1))
02580 RETURN
02590 END
```

Lines 2510-2580 are a subroutine that calculates the sector from which the soil sample was collected. In the years 1967-1971 sectors in the experimental plots were different. In these cases a random integral number in the range 1-10 inclusive is generated (line 2570) and used thereafter.

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TOWARDS AN ENERGY BALANCE SHEET FOR THE NOVA SCOTIAN AGRICULTURAL FOOD SYSTEM

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Measures are made of the Nova Scotian energy exchanges as the broad dilute field of incident light becomes concentrated into mature plant and animal food crops. The net distribution of the on-farm energy inputs (excluding solar energy) are: 60% fertilizer (which is 60% lime, 40% NPK); 30% fuel and machinery; 10% remainder. There are also post-farm inputs of factory processing, transport, wholesale and retail handling, and home preparation. The on-farm part of the total energy cost varies from less than 10% (for processed potatoes) to 40% (for apple juice). The total annual energy costs to supply human food and animal fodder from the region are of the order of 2000 kcal x 10^9. The most efficient products are grains, which have a food value of 900% of input energy; the least efficient are poultry, whose food value is only 10% of the energy required to produce it.

Introduction

For agricultural prospects as for so many of our other activities, energy costs have become a substantial concern. Before the oil price rises which began in the early 1970's, the direct ends, or derivatives of agricultural investigations had such concerns as the following:

1. Biological and technological. Which plants and animals can be most suitably and efficiently grown in our region and what new varieties can be introduced?

2. Economic. What is the financial future of the farmer and the processing and handling industries in the face of changing monetary prospects?

3. Sociological. Is increased farming to be encouraged as compared with other natural-resource industries? How many workers are to be placed on the land?

4. Political policy. Decisions on the use of land, whether for agriculture, forests, roads, urban intrusions. Policy towards home-grown versus imported products.

During the last decade a new consideration has arisen which deals with energy receipts and expenditures and how their balance can be improved, or how they are likely to be altered outside our area in ways which might benefit Nova Scotian agriculture. The transport of Californian fresh products to our market offers an example. As fuel costs increase, the balance may shift in favor of locally produced food. The energy costs associated with food production, distribution and processing should be understood in order to determine where energy conservation measures are likely to have maximum impact; where measures intended to enhance or regulate agriculture may have high energy costs; and how energy consideration may influence decisions and prosperity of individual farmers and processors.

What we are attempting here is to develop a Nova Scotian energy balance sheet for the agricultural sector. It is hoped that this may be used to examine changes and offer recommendations about the future course of our agriculture. The point of view of the present analysis is that of Odum (1971) who is concerned with the applications of power, which in turn is defined and measured as the rate of flow of useful energy. In agriculture the essential aim is to bring about a change from a broad dilute field of incoming light into the concentrated energy of food which is needed by man; the approach we use to examine the process is by measurement of the energy exchanges as the crops mature. The flow is measured in time units; in this paper the selected energy units are G or gigaCalories or billions of kilocalories, as used in the Nova Scotian agricultural system annually.

Table I. Variation in energy distribution to bring a fixed quantity (say, 1 kg) of food to use. To facilitate comparisons, the on-farm costs have been called 100. Actual on-farm costs in kcal kg^{-1} are 752 for potatoes and 516 for apples. (Whittlesay & Lee, cited from Agriculture Canada 1977.)

	Potatoes			Apples			
	Fresh	Frozen	De-hydrated	Fresh	Dried	Juice	Sauce
On-farm production	100	100	100	100	100	100	100
Processing	–	591	836	–	97	32	159
Transportation	241	154	44	219	33	77	168
Wholesale and retail trade	10	140	19	17	6	11	28
Home storage	–	51	–	53	–	37	–
Home preparation	390	128	112	–	–	–	–
Relative totals	741	1164	1111	389	236	257	455
Absolute totals (kcal kg^{-1})	5560	8730	8335	2015	1225	1330	2360

Limitations on the energy flow approach are acknowledged. The estimates of energy transfer and dissipation are, at this stage, rough approximations. Consideration of calories alone is not relevant to certain issues, such as nutritional quality of food. There is also the perplexing matter of money-energy relationships. Money has been described as a feedback loop which joins some parts of the system, in which it moves in the opposite direction to energy; we obtain food by dispensing money and receive money in return for dispensing our energy as work. Thus money provides a means for organizing the directions of energy movements. Money circulates, whereas the flow of energy is undirectional since energy is continually running down until the sun rebuilds it again into plant life.

As an example of the energy-money relationship we may consider the production of a kilogram of potatoes which when eaten furnishes the body with some 900 kcal, a value that has no corresponding monetary unit. To produce the crop the main source of energy is the sun of which the small fraction (less than 0.1%) which is utilized is also unrelated to money. To augment the sun the farmer adds fuel, pesticides, fertilizers, etc. which cost 750 kcal, a group of costs which could, if desired, be converted to the fluctuating dollars of the moment. Between harvesting and eating, the potatoes require processing, packaging, shipping, marketing, and cooking which cost on the average an additional 700 kcal. For the whole sequence then, it is clear that while a balance sheet can be drawn up in terms of energy, and that some items have a current exchange value into money, it is not feasible to make the whole equation realistic in terms of dollars.

The difficulties of comparing different kinds of energy inputs (solar energy, fossil fuels, animal power) cannot be completely overcome by conversion to common calorific values. Energy consumption at each of the producer, processing, and distribution stages has its own distinctive economic characteristics which influence its potential for altering energy. The energy complexities associated with product type are also significant. Table I illustrates the variation in both total energy cost and its distribution for different potato and apple products.

Despite these various limitations to the energy balance approach, we feel it offers potential to stimulate a renewed interest in traditional forms of Nova Scotian agriculture as well as a more critical review of various provincial and federal agricultural support programs. To such, an energy overview provides an organizing focus for many of the ecological studies which should be undertaken if we are to improve, in any major fashion, our agricultural production. Certain suggestions will be made for changed use of the Nova Scotian energy now being consumed in the food system. Above all, however, it is intended to stimulate further research. The unevenness of the information presented is indicative of the need.

Energy Inputs and Outputs

Average input costs which are necessary to produce, process, and distribute Nova Scotia farm products have been derived from several references (Agriculture Canada 1976; Downing 1975; Henig & Schoen 1975; Hirst 1974; Jensen & Stephanson 1975; Lovering & McIsaac 1976; Ontario Institute for Agrologists 1975; Pimentel et al. 1973; Timbers 1977). In the home and in commercial outlets the storage and cooking of food uses about one-third of the energy required by the system. Transporting and selling the products account together for one-quarter, and processing for another one-quarter of the cost. Only 20% of the energy is used to produce the crop on the farm. Over much of Canada the dominant on-farm input is fuel for machinery, but Nova Scotia, like Prince Edward Island and parts of Ontario, uses a much higher proportion (60%) for fertilizer (Downing & Feldman 1974; Tables III, IV).

Individual products show wide variability from the foregoing averages; for example, animal products may require very high on-farm inputs (Table V). The processes preparatory to consumption also vary widely, as the examples in Table I show. With fresh potatoes the dominant costs lie in home preparation and transport, while the handling of "fast food" preparations adds large processing costs which bring up the total energy to more than 10 times the on-farm input. For fresh apples, more than half the energy goes for transportation; for the dried product on-farm and processing make up over four-fifths of the costs; for juice the chief inputs are on-farm and transport; while processing and delivery make apple sauce the most costly energy user of the family of apple products.

Figure 1 represents energy flow in the Nova Scotia food system. It is adapted from Downing's (1975) picture of the energy flow in the Canadian food system. Downing's divisions and percentage breakdowns were used for the most part. For example, in the original energy breakdown (first left vertical set) Downing suggests that 20% goes into fodder, and 60% into feed, food, and fiber. Downing's proportions were retained throughout Figure 1 with a few exceptions where Nova Scotia was thought to differ from the Canadian average. Nova Scotia Agricultural Statistics (1975) show that exports are lower and imports higher than the national average. They show that at least 50% of animal feed is imported, and for human food we have placed imports at 60% (470/790 at extreme right of Fig 1). In Figure 1, a few totals and some key intermediate numbers have been entered to help provide the thread of the energy chain from fertilizer to food. The numbers are derived from the input in which we had most confidence, namely fertilizer. Details of the energy calculation for fertilizer are shown in Table II in which column 1 and column 2 come from Tables 70 and 71 of Nova Scotia Agricultural Statistics (1975); column 3, which in-

Table II. Annual use of fertilizer on Nova Scotia farms.

	Annual N.S. use (5-yr avg. tonnes x 10^3) 1	Nutrients (% of wt) 2	Energy (kcal/kg) 3	Annual N.S. cost (kcal x 10^9) 4
Nitrogen as ammonium nitrate. Energy as kcal/kg N	3.94	43	21,650	37
Phosphate as triple super phosphate. Energy as kcal/kg P_2O_5	4.82	43	4,842	10
Potassium as muriate of potash. Energy as kcal/kg K_2O	4.85	43	3,519	7
Lime. Manufacturing and transport costs as kcal/kg	54.81	-	1,512	83
TOTAL				137

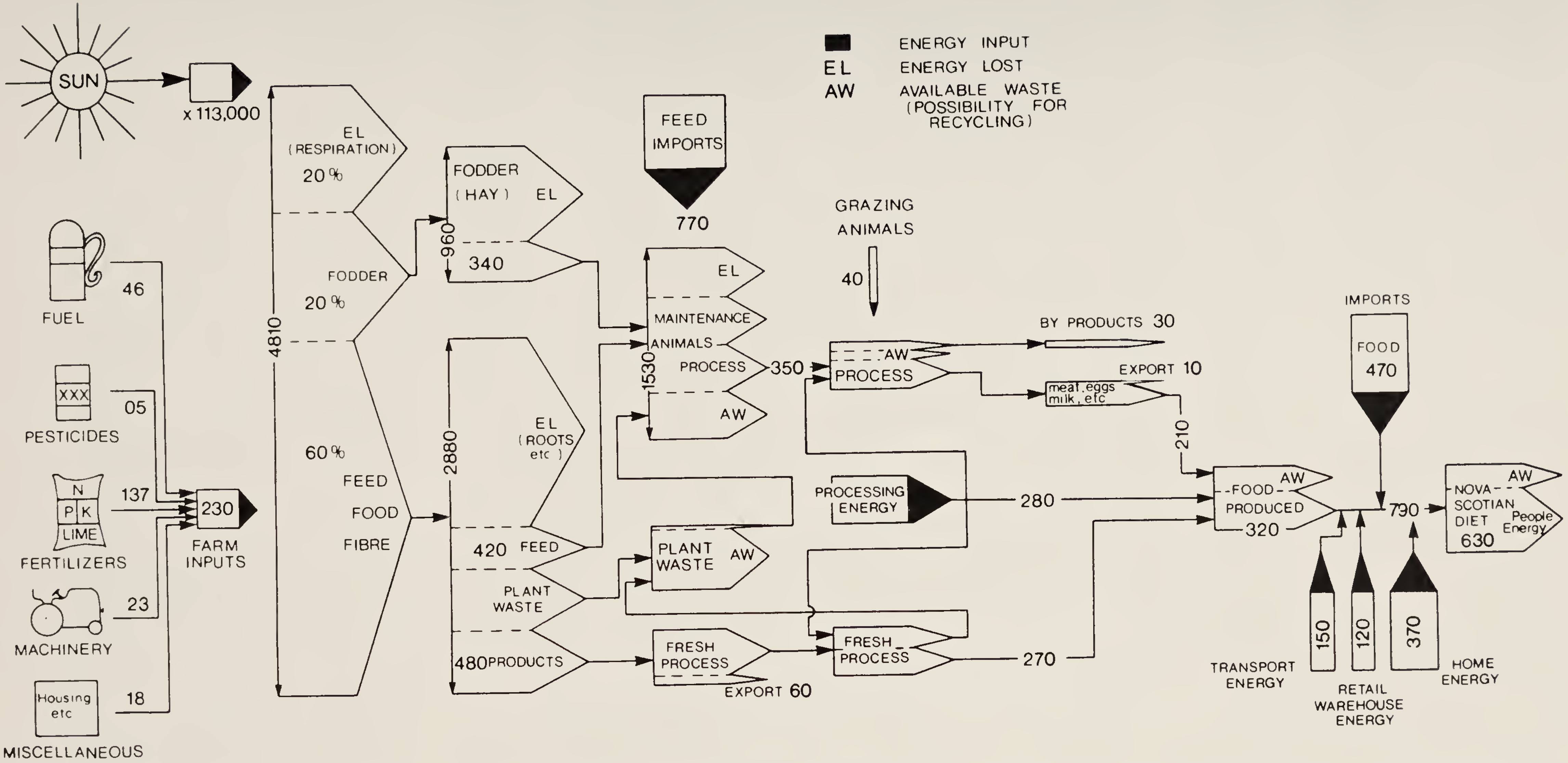

Fig 1. Energy flows in the Nova Scotian food system per annum. Width of arrow base indicates relative amounts of energy. Numbers are kcal x 10^9.

cludes production energy cost of the fertilizers, including fuel, transport, etc., came from Southwell and Rothwell (1976) and Leach (1975, cited from Jensen 1977). Column 4 calculates the total kcal value for fertilizer of 137, which was entered as the initial number on the large chart, Figure 1.

In the absence of direct Nova Scotian values, the remaining inputs shown in Figure 1, for fuel (46), pesticides (5), machinery (23), and miscellaneous (18) were adopted after comparing numbers in the literature. Some of the numbers, as percentages, are given in Tables III and IV, and those accepted for Nova Scotia are in Table III, column 9.

The total farm energy input of 229 x 10^9 kcal is in close agreement with the corresponding number of 248, adjusted by us for Nova Scotia from the Prince Edward Island estimate of Lovering and McIsaac (1976) which was based on Prince Edward Island acreages.

As the tables show, there is across Canada a good deal of variability in the reported distribution of inputs, which differ according to regions, soil conditions, moisture, type of crop, and treatment during growth and after harvest. Any single high input will distort the percentage tables. For instance, in Prince Edward Island the curing of tobacco is reported to use half the total input energy; also their seed for potatoes is unusually costly. In Table III some Prince Edward Island crops are compared to show how their percentage distributions are affected by the energy totals required. However, they average out quite similarly (Table III, columns 7 & 8) whether direct means are used or those weighted for total demand.

In Nova Scotia as Table II (column 4) shows, the exceptional cost is for lime whose annual use is increasing with the subsidy program (vide infra). To show how lime contributes to making up the Nova Scotian list, compare Table III (column 9; the actual adopted figures) with Table IV (column 1), which gives figures as they would have been if Nova Scotian soil had not required lime; even omitting lime, fertilizer is still high. Several authors have suggested that, as our tables indicate, fertilizer accounts for a high proportion of on-farm input in agricultural systems similar to Nova Scotia (e.g. Prince Edward Island, parts of Ontario): (Downing 1975; Hirst 1974; Ontario Institute for Agrologists 1975, cited from Agriculture Canada 1976; Steinhart & Steinhart 1974; Whittlesay & Lee 1976). In the western provinces on the other hand, and for Canada as a whole which is strongly affected by the prairies, the dominant energy input is for fuel (Timbers 1977).

To sum up: after a careful, even though not statistically quantifiable, study of the records, we have adopted for Nova Scotia the relative values shown in Table III (column 9) which, when put into absolute numbers, are the quoted farm inputs listed on Figure 1.

The next step was to establish a number which would place on-farm inputs as a percentage of the total food system costs. Literature estimates vary from 15 to 24 and were rounded to 20% for this study (references cited above). Similarly, other components of the food system had probable input percentages which have been entered on Figure 1.

The annual energy input applicable to Nova Scotia production, as shown on Figure 1 is about 1600 x 10^9 kcal or, in the more usual weight-watcher's terminology, 1600 billion Calories. The total is derived by adding up the black arrow numbers on the large diagram (excluding sun energy) but using for the final 3 (transport, warehouse and home energies) only 40%, which is the part applicable to Nova Scotia products. If full market and home costs are included, the total input becomes about 2000, and with imported food, it goes up to 2400 billion Calories.

Table III. Prince Edward Island percentage farm energy costs for several crops, based on acreages, showing direct averages and averages adjusted for total inputs (Lovering & McIsaac 1976[1]). The accepted Nova Scotian inputs are also shown, although they were derived from comparisons with Table V as well as with Prince Edward Island.

	1 Potatoes	2 Other vegetables	3 Silage corn	4 Cereals	5 Hay	6 Pasture	7 Mean	8 Mean weighted for total energy inputs	9 Nova Scotian values as used
Relative total energy inputs, Potatoes as 100	100	78	50	32	11	7			
Fertilizer	48	74	61	55	53	92	64	60	60
Fuel	25	18	29	25	40	8	24	24	20
Machinery	4	2	4	4	6	-	3	3	10
Pesticides	7	5	4	2	-	-	3	5	2
Other, e.g. drying grain, curing tobacco, etc.	16	1	2	14	1	-	6	8	8
TOTALS	100	100	100	100	100	100	100	100	100

[1] The absolute values in this paper are too high by a factor of 10. Comparisons of percentages are acceptable.

The whole growth system is set in motion by the sun, whose input is several orders of magnitude greater than that provided by farmers (Table VIII). The sun's energy, being a given constant, has not been subject to further analysis here.

Comparison may be made between the initial farm energy cost of 230 and the useful harvest. (It is unnecessary to consider human and animal labour which are quite inconsiderable parts of the energy system). The plant harvest for human use is valued at 480 x 10^9 kcal to which the animal feed and fodder adds 420 + 340. The total of 1240 is 540% of the on-farm input, a strong energy profit.

At this first stage the primary on-the-land investment has been parlayed into a more than 5-fold energy gain. From here on it is downhill all the way as further in-

Table IV. Hypothetical Nova Scotian energy inputs as they would compare with other regions where less lime or no lime is used as fertilizer (cf. Table III, col. 9).

	1 What the accepted Nova Scotian inputs would become if lime were omitted	2 Ontario (Downing 1975)	3 Ontario (Ont. Inst. Agrologists, cited from Agriculture Canada 1976)	4 Saskatchewan (Downing 1975)	5 All Canada (Timbers 1977)
Fertilizer	35	31	57	4	15
Fuel	33	44		71	68
Machinery	16	8		8	5
(Fuel plus machinery)	(49)	(52)	33	(79)	(73)
Pesticides	3	?	2	?	1
Other	13	17	8	17	11
TOTAL	100	100	100	100	100

vestments are made to get the food into more valuable forms, get it to market, and get it into use by consumers. The 1240 x 10^9 kcal at this initial stage are in the form of fodder, feed or plant products to be further refined. The larger portion, 60% of the initial energy available, is cycled into animal food. The remaining 480 x 10^9 kcal (40%) is further processed into feed energy which is still available for consumption. At this point, plant food for humans is ready for processing, with a final efficiency of 56%. Animal feed requires further inputs and there are also maintenance costs before processing, with consequent reductions in farm efficiency.

The upper half of Figure 1 as well as Table XI, deals with the energy relations for beef, hogs, poultry, eggs, dairy products, and their sustaining feed plants. The calorific values of fodder and feed are derived from standard measurements of animal calorimetry, where maintenance is a balance between assimilated inputs and absolute loss as CO_2, plus available waste as manure and urine.

Processing energy (280 x 10^9 kcal) acts on food which comes from the farm, while the post-farm outputs include industrial power and machinery (60% on the average), together with such commercial items as steel and aluminum cans (24%), glass containers (9%), and paper packaging (7%) (Steinhart & Steinhart 1974).

It is assumed that the food produced as plant and animal products (270 + 210) should have the processing and handling costs prorated to 180 plant output and 140 as animal food (see chart of derivative outputs, Table V). Processing costs will be respectively 160 and 120 for the total of 280 on the chart. Finally, there are large energy inputs required to get the food transported and handled and onto the Nova Scotian table. As mentioned previously, 40% of these final inputs or 256 kcal (plants 140, animals 110) are used up by Nova Scotia-produced food. The foregoing chain of energy events is summed up in a later section.

Direct Measurements

In the previous section, the averages of Canadian farm energy inputs have been taken as a base, and modified to make them applicable to Nova Scotian conditions. The numbers were then recalculated to correspond to the area under cultivation in Nova Scotia with results as illustrated in Figure 1. We turn now for comparison to an independent source of information, namely the annual presentation of data for individual crops as published by the Provincial Government (Nova Scotia Agricultural Statistics 1975). Production is listed in English units which have been converted to metric weights and calorific energy values. Detailed results are given in Tables X and XI of the appendix (with assumed or interpolated numbers in brackets). The derivation of input energies makes use of information from Heichel (1976), Jensen and Stephanson (1975), Southwell and Rothwell (1976), and Whittlesay and Lee (1976). The nutritional values given by these authors were supplemented by the Geigy tables (1956), for human food (Table XII). All sources were compared to secure an accepted value, although there are still many information gaps. Table V is a summary of the direct observations.

Of the 3 columns of figures in Table V, the left one gives the annual energy production cost for the Nova Scotian farming area in kcal x 10^9. The centre column gives the food or fodder value of the product in the same units. In the right column, the food value is expressed as a percentage of the energy input. From the percentage column, it is evident that great variability exists among farm crops. Those with the highest yields are wheat for humans, and pasture, hay, silage, and grains for animals. These have output values reaching 750% of the energy-inputs, which is almost 6-fold that for vegetables and fruit, whose average comes to only 135%.

The second section of Table V deals with post-farm energy costs for food plants.

Table V. Summary of direct observations on food destined for human consumption. Numbers are Nova Scotia annual totals taken from Tables X and XI of the Appendix, where their detailed derivations are given. Outputs are calorific food values from standard sources, for which a list is assembled in Appendix Table XII. Numbers are rounded and not necessarily in complete agreement in different places.

HUMAN FOOD PLANTS	kcal x 10^9		Food energy as % of input energy
	Input cost	Output	
1. FROM THE FARM			
Wheat	2.1	15.1	720
Potatoes	20.3	23.0	112
Carrots	5.5	4.9	90
Other vegetables	4.0	2.5	65
Apples	21.6	24.1	110
Blueberries	1.4	2.8	200
Other fruit	0.6	1.0	150
Total	55.5	73.4	132
2. POST-FARM. Processing, Commercial handling, and home preparation			
Wheat: proc. 2.0; com. hand. 0.7; home 3.5.	6.2	15.1	245
Potatoes: proc. 72.5; com. hand. 43.7; home 54.4.	170.6	23.0	14
Other vegetables: proc. nil; com. hand. 23.8; home 37.1.	60.9	7.4	12
Fruit (82% Apples): proc. 8.2; com. hand. 33.9; home 11.7.	53.8	27.9	52
Total processing & handling	291.5	73.4	25
Total plants	347.0	73.4	20

ANIMAL FOOD

3. ON-THE-FARM FODDER

Pasture, hay, silage	154	1214	790
Grains	16	122	760
Imported feed	766		
Total	936		

4. PROCESSING AND HANDLING OF HUMAN FOOD FROM ANIMALS

Numbers refer to edible portions
after processing losses.

Beef	179	23	13
Hogs	119	30	25
Poultry (including 5 to 10% for eggs)	232	20	9
Dairy products	244	100	41
Total	774	173	22
Total animal feed	1710	173	10
Grand total: Human food, plant plus animal	2059	246	12

The input cost has been subdivided into the parts for: (a) commercial or factory processing; (b) transportation plus wholesale and retail handling; and (c) home costs of refrigeration, preparation, cooking, and loss at the table. The superior efficiency of wheat is even more striking here than on the farm. The post-farm yield of wheat per input energy unit is from 5 to 20 times that of other plant food products. The major Nova Scotian plant crops are potatoes and apples. Apples are the only fruit crop for which valid in-and-out costs are available. (Heichel 1976). Blueberries, most of which are exported, make up less than 4% of the edible plants.

Section 3 of Table V deals with combined pasture, hay and silage, plus grains, all of which are among the highest level producers. Pasture is difficult to compare because of its seasonal and qualitative variability. The positive output ratio of on-farm plants is largely cancelled out by imported feed which we have placed as an energy debit.

As to processing-handling (Section 4, centre column) dairy products have maximal food value (100) and efficiency (41%), while poultry is the lowest (20 and 9%). The latter numbers are attributed to the low calorific values of young birds (see food values in Table XI, column 4). On an evicerated dressed-weight basis 90% of our poultry produce is chicken and fowl, of which 90% is chicken (Nova Scotia Agricultural Statistics 1978). Much of the chicken is further processed for the fast food trade.

In Table V and in the Appendix Tables, no allowances have been made for product losses which may occur during post-farm processing-handling and household operations. For fresh meats, fruits, and vegetables, losses may be considerable, while for packaged commodities rejections are probably negligible. According to Copping (1976), the wastage factor for household food may include cooking, domestic loss of nutrient, inedible bones, outside skins and leaves of fruits and vegetables, and plate waste. Obviously, societies will differ in their food rejections; in Britain annual lists have been compiled of food categories, each with its special nutrient conversion factor. British wastage in the household is taken at an inclusive figure of 10%, we omit Nova Scotian factoring as premature.

In addition to the crops listed in Table V, the published statistics show several minor fruits and vegetables, honey, greenhouse operations, etc. There are also non-food items including wool, tobacco, and pelts. Forest products such as Christmas trees and maple products may also be included. None of the foregoing impinges importantly on energy considerations.

Direct and Indirect Production Estimates Compared

In this section, the values derived above from the energy flow chart, (Fig 1) are compared with those which come from direct Nova Scotia Agricultural Statistics (1975). As a first step, both sets of values (Table VI) have been related to their final output calculations as human food. We begin with the bottom line which is an approximation of expected human consumption. Assume that each of the 800,000 Nova Scotians consumes 3000 kcal for 365 days. This gives an annual food use of 880 x 10^9 kcal. Provincial agricultural production as 40% of food eaten, comes to 350 x 10^9 kcal (bottom line of Table V, a figure which is not far from the 320 calculated from Figure 1 for food sent to market) or 248 (food supply as added up from Nova Scotian statistics on individual products; see total outputs on Table VI).

The second row from the bottom of Table VI refers to the extreme right of Figure 1 in which it is noted that 20% of the food prepared for the table is discarded so that only 252 of the 320 x 10^9 kcal produced in Nova Scotia are finally eaten. As calculated in a previous section dealing with Figure 1, final plant product energy output at 180 is higher than final animal product energy output at 140. The direct Nova Scotian statistics show animal food output to be greater (74 and 174 respectively; see Table V). The low value of 74 for plants is probably correct and may reflect the negligible cultivation of wheat for bread in Nova Scotia. Our major grain crop other than hay, is oats for animal consumption. Figure 1, which shows plant production dominant, probably reflects the western Canadian average where grains dominate. (Downing 1975).

According to Table VI, input costs on the farm are quite small for plant products (90 and 56 by the 2 methods) being some 4 times exceeded by processing and handling costs (ca. 300) on the route to the human digestive system. The more important place to seek energy-saving economies would evidently be in post-farm operations.

Animal products have the opposite relationship, with on-farm costs being greater than those for processing and handling. As derived from Figure 1, the ratio is 7 while

Table VI. Relation between food consumed by Nova Scotians and agricultural production. Numbers in the left section are from Figure 1 with on-farm values adjusted to omit exports. Numbers in the right section are from Nova Scotia Agricultural Statistics (1975), average of 1971-1975.

	CHART DERIVATIVES			DIRECT PRODUCT OBSERVATIONS		
	kcal x 10^9			kcal x 10^9		
	Input cost	Output	Output as% of cost	Input cost	Output	Output as % of cost
PLANT PRODUCTS						
1. From the farm	90	180	200	56	74	132
2. Processing, handling and home	300	180	60	294	74	25
Total	390	180	46	350	74	20
ANIMAL PRODUCTS						
1. From the farm	1710	140	9	935	174	19
2. Processing, handling and home	230	140	61	775	174	22
Total	1940	140	7	1710	174	10
Total plant plus animal	2330	320	14	2060	248	12
Kitchen to body, 790 & 630 of which 40% raised in Nova Scotia (Fig 1)	316	252	80			
Rough guess of Nova Scotian consumption is 900 of which 40% is locally produced		350				

the difference as seen from direct observations is only 1.2, a discrepancy not explicable now. Input costs for animal feed are especially high in Nova Scotia because of feed imports of grain, which count as outputs on the prairies but as imports here.

The processing and handling costs, whether for plant or animal products, are greater than the energy value of the food delivered to the consumer. Expressed as a percentage, the food value is only some 60% of the post-farm cost (chart derivatives) or 20 to 25% (direct observations). Stated otherwise, the processing-handling costs use up perhaps 2 to 5 times as much energy as the food they deliver.

For the individual product observations on the right half of Table VI, we did not have a breakdown into factory, selling, and home costs, but calculated them from figures of Whittlesay and Lee (1976). The calculations on the direct or recorded Nova Scotian data may be found in Appendix A.

The 2 right-hand columns in Table VI express the energy output from the plants and animals as percentages of inputs. Plant products on the farm have maximum yields of 200% of input from Figure 1, a value which is elevated by grain (see the first lines of Table V comparing wheat with other plants). Direct Nova Scotia values on the right side of Table VI show 132% gain, because wheat is not very important. As to animal food, we get, by the 2 methods, 9 and 19% of the energy that the farm puts in. Farm energy, then, is between 7 and 22 times as effective for plant production as for human food of animal origin.

For the combined operations of on-farm and processing-handling we can expect to get back 20 to 45% of the plant costs as food, while animal food represents only 7 or 10% of its costs.

Discussion

Canada as a whole uses 10% of its total energy for the food system, a number which is derived from Downing's tables (Agriculture Canada 1977). Downing gives on-farm totals, to which he states there should be added almost 3.5 times as much energy which is utilized to process and handle the crops. In the United States, the food system uses 16.5% of the total national energy output (Agriculture Canada 1977, Table 6).

For Nova Scotia, the total energy consumption (average for 1978 & 1979) is about 65,000 kcal x 10^9 (Nova Scotia Energy Update 1979). The agricultural input costs (bottom lines of our Table VI) average a little over 2000 kcal x 10^9 which gives 3.4% of the provincial total; about the same as the contribution of hydro power to the Province. Nova Scotia's low percentage figure reflects the smaller place of agriculture here, compared with the central growing areas of the continent. In Nova Scotia, depending on the crop, from 10% to 40% of the energy of the system is used on the farm, and the rest goes into processing and handling. Of the initial farm inputs the largest is for lime followed by fuel and machinery, NPK fertilizers, etc. In addition to the foregoing and more than 3 times as great are the imported feed grains. Taken together, the Nova Scotia on-farm costs from outside come to some 10^{12} kcal, a sum which is nearly doubled when we include the feed and fodder grown on the farm for the animals. The food value from human edible carbohydrate may be twice the farm input cost, while for the available protein-fat complex from animal stock the output is only about one-fifth to one-tenth of the cost.

Processing and Handling

Processing costs for plant products (examples in Table I), are usually several times as great as the initial farm inputs. Major processing contributions include industrial power and machinery as well as metal, glass, and paper containers. On the animal side, the dominant energy costs associated with processing are for dairy products and poultry and the slaughtering of meat. Plant and animal products are about equally demanding for refrigeration and storage, followed by the familiar retail activities, then by home storage and preparation. For products grown in Nova Scotia, the approximate annual processing and handling costs for plants total 300 and for animals 350 x 10^9 kcal. The energy importance of post-farm operations can be further underscored by consideration of a so-called agriculture-related component not developed in the present study. Conspicuous components in Nova Scotia would include alcoholic and soft drink bottlers, bakers, and confectioners. Elsewhere in Canada the list would include as well, rubber products, sugar refiners, flour and breakfast cereal producers, and shoe and leather workers. We do not have figures with which to construct a quantitative breakdown of the Nova Scotian component of processing and handling which would correspond to the on-farm portion of the story as illustrated in Figure 1. The development of individual industry costs for dealing with food and related products together with recommendations for energy economies must be considered a matter of high priority.

Tables VI and X show the post-farm division of plant energy inputs into processing, commercial handling including transportation, and home preparation (Agriculture Canada 1977, Tables 32 et seq.). We lack the information necessary for a similar treatment for human foods of animal origin. As so much of the energy associated with food systems is tied to post-farm operations, it is tempting to focus studies and energy conservation programs off the farm. In fact, we concentrate the remaining discussions towards on-farm topics for 3 reasons. First, there is a definite need to consider how vulnerable individual farmers are to energy imperatives. Secondly, it is of interest to consider not only present-day patterns, but also future stages of development when processing, etc. may be much more efficient while primary producers are called upon for dramatically increased yields. Thirdly, the problems of farm-level energy conservation appear to be more complex to deal with as they involve ecological, social and political complexity, in addition to the shared problem of economic feasibility.

Savings on Farm Inputs

Energy improvements in farm machinery are likely to follow patterns developed in the United States. An example is the conversion to diesel-powered farm tractors which now make up more than 85% of new purchases there. Diesel machines use 27% less fuel than those powered by gasoline to do the same amount of work and their fuel is generally less costly. Diesel tractors, however, cost 11% more to buy than those powered by gasoline. Here we have an increased initial cost to be compensated by later monetary as well as energy savings. Other farm machinery shows corresponding fuel relationships. Additionally, a more critical use of farm machinery with energy savings in mind can effect some 15 to 20% reduction (Friedrich 1978). For conversion of the above to Nova Scotian savings, a look at the left end of Figure 1 shows that the change to diesel fuel would save some 125×10^9 kcal annually and other savings in machinery would add another 40×10^9 kcal. These are not inconsiderable quantities and they make a good case for financial incentives, demonstrations, and educational programs.

Over the manufacturing costs of fertilizer the farmer has, of course, no control; his only place to look for economies there lies in diminished use. Taylor (1976) offers a table of energy-saving tips, beginning with an annual soil analysis. We may first mention lime which makes up 60% of our calorie costs (Table II). Since the Province is helping to finance an increasing use of lime, it is doubtful whether significant savings in its use are yet to be achieved. Incidentally, the costs of lime production are expended in Nova Scotia which is a socio-economic consideration. The other 40% of fertilizer energy, mainly nitrogen, has more complicated and shorter term relations than lime. Here research and development are needed to establish the best dates of application as compared to dates of planting and to rates of growth and applicable to various major crops. Taylor also observes that the application of starter fertilizer through the planter or drill is more efficient than broadcasting. Another observation (Friedrich 1978) is that the effectiveness of fertilizer declines with increase in the quantities used, which means that there is an optimal economic rate for the farmer which depends on a comparison of crop production with dollar costs. The savings outlined might together be expected to reduce use of NPK by 25% which would amount in Nova Scotia to 13.5×10^9 kcal.

In recent years, strong objections have been raised about the undesirable side effects which accompany the use of pesticides to control crop losses. An evaluation of the debate would be outside the scope of this paper. In any case, local use amounts to only 2% of farm inputs (Table III) out of which any proposed energy savings would be minor and would be greeted with scepticism by many farmers. We might guess at a saving in the order of a mere 100 kcal.

The bottom line of Table III, 'Miscellaneous' or 'Other', takes in a variety of items including labor, the use of energy in the home, seeds for planting, the drying of cereal crops and tobacco, etc. Its total value is only 18 x 10^9 kcal and obvious potential savings are too small to warrant an estimate now.

To sum up: the savings above come to 179 x 10^9 kcal, of which more than 90% is in fuel and machinery. As a contribution towards solving the national energy problem, it is a rather small item, some might say scarcely worth the effort. However, as a contribution to farmers of the province, it may be essential or vital to their economic survival. Domestic farming has such a high social priority that the level of effort required to secure these savings is fully justifiable.

Any energy-saving changes in farming procedures will be complex compromises between competitive interests. One set of conflicts is national, advocating all-out production of what each region does best and an uninterrupted supply of food, both of which demand extravagant energy. By contrast, the maintenance of environmental fitness demands energy restraint. Then there are the provincial socio-economic objectives of variety and self-sufficiency and there is the demand of consumers for reasonable prices. Added to all these are the necessity of the farmer to receive a reasonable living and the limits of available federal and provincial resources to implement and supervise proposed programs. Clearly the obstacles to energy conservation are formidable.

Energy problems might be divided into macro (survival of the nation) or micro (physical or economic survival of each individual). The farmer, in his production of a continually consumed renewable resource, is a major factor in the national problem. As an individual, the increasing energy costs on his farm offer a threat to his personal economic survival. His continued or increased success is thus doubly important.

Non-food Products

There are some half-dozen such items listed (Nova Scotia Agricultural Statistics 1978), led by two luxury products. Energy values are not available so we mention farm receipts in dollars as percentages of the Nova Scotian totals for 1978, which are: greenhouse flowers, 5%; mink and fox pelts, 2%; all others together, less than 0.5%. Shorn wool is only 0.05%. We have not given any special treatment to these products either in processing or marketing energy allowances.

Size and Diversity of Production Units

From historical settlement patterns, Nova Scotia has inherited a small mixed-farming unit of production. There has been a noticeable trend toward farm consolidation and more capital-intensive production processes. Thus in a quarter-century since the war (1951-78) Nova Scotian farms declined by consolidation to 25% of their earlier number, and at the same time, the average size increased from 50 to 90 hectares while the improved land on the farms went up from 20 to 25% (Nova Scotia Agricultural Statistics 1978). Nonetheless, in Nova Scotia the family farm, part-time farming, and smaller, less capital-intensive units of production, still exert an important influence over Nova Scotia agriculture. Although the average size of our farms is about the same as in Ontario (Geno & Geno 1976), the number of hectares improved by active cultivation has, until recently, only been one-third the

Table VII. Relation of farm size to income (McMahon 1976).

	Up to $2500	$2500 to $5000	$5000 to $10,000	$10,000 and over ($25,000 median)
Number of farms	3400	747	621	1200
Average number of improved hectares	15	25	35	60
Dollars/improved hectare	100	150	200	400

Ontario level. Since about 1960, the amount of improved hectarage per farm has been rising in Nova Scotia and now approaches one-half the Ontario level.

Table VII is a breakdown of some 6000 Nova Scotia farms into improved hectarage and gross income. Data are from the 1970 census. The figure for dollars per hectare (bottom line of Table VII) is subject to considerable individual variation as well as inflation. Included under each farm income category are some producers who specialize in animal production, certain types of which (e.g. chickens, hogs) are grown on limited plots of land, often utilizing imported feed. Hence, the yield per hectare for such operations will be considerably greater than for a farmer who specializes in cash crop production. As well, the relatively low dollar yield per hectare in the $2500-or-less category of farm income is partially attributable to large numbers of part-time farmers, some of whom underutilize their land. Nonetheless, it is abundantly evident that larger farms yield more dollars per hectare than small ones. In the past, high income per hectare would have been the measure of success. Today, however, the enquiry is whether the gain in extra dollars per hectare is at the expense of importing petrochemical energy, and whether acceptable financial returns may not be achieved by practices which require less extravagant use of fuel. Any definitive presentation of aggregate energy flows or possible sources of energy savings should take into account the size, diversity, and scale of production units. The trend of contemporary farming is towards highly mechanized, capital-intensive operations, with a parallel reduction in human and animal labor, which have today become negligible energy costs on the farm. The replacement of labor with capital has reduced the number of farmers to such an extent that currently the outside workers who produce the agricultural inputs outnumber those on the farms by about 2 to 1. It is estimated that in the United States one man can take care of: 60,000-75,000 chickens; 5000 head of cattle; 50-60 milk cows (Friedrich 1978).

Land Use and Crop Choices

The whole system is set in motion by the sun's energy, which may be compared with other inputs. From the sun, 2.6×10^{15} kcal falls annually on the farms. Other inputs are given in Table VIII and show a range from 0.01 to 0.2% of the solar level. In general, photosynthetic efficiency will vary according to the region, the kind of crop selected, and the soil treatment. When considering Nova Scotia, we take the average climate and sunshine as constants, while the soil shows, of course, regional differences which are further adjusted for each desired crop by the primary and special additives, fertilizer, lime, pesticides, etc. The numbers set down in Figure 1, 4810, 230, 1240, etc., represent mean efficiencies; later studies will be required in order to characterize individual crops and regions of the province.

Table VIII. Other energy inputs compared to the sun.

	kcal X 10^9	Percent uptake of sun's energy
Farm inputs.	230	0.01
Total harvest, including respiration which represents the portion of the crop used up during the summer. Unused portions are also included.	4810	0.20
Ongoing or useful harvest, i.e. hay, feed, fruit, and vegetable products (340 + 420 + 480 at left of Fig 1).	1240	0.05

Wheat is much the most productive commodity to grow, with an on-farm efficiency almost 6-fold that for vegetables and fruit. In post-farm operations, wheat is more than 10-fold better than the rest. The difference is presumably because there is little cost associated with the use of baker's bread in the home (and the good old days when the "bread man" labored to deliver it to the home are remembered only by senior citizens). Grains, moreover (Table XII) are given a much higher nutritive rating than vegetables, wheat being about 4000, potatoes 750-900, cauliflower 300, and pumpkins 150 kcal kg^{-1}. We do not grow much of our own wheat, whose production is greatly exceeded by apples and potatoes. Our major grain crop is oats which are for animal feed. In early days when the settlers lived largely on locally grown oatmeal, the efficiency of food distribution would have been much higher.

There is a necessity to determine for specified areas, what kinds of land use will offer the greatest yields of useful energy. Of our unimproved or marginally developed land, some is potentially competitive as farms, perhaps to grow crops for industrial alcohol while some forest land may be competitive with pulp uses for the same purpose. Clearly the distinction between agriculture and forestry is becoming a thing of the past.

Photosynthetic efficiency is a factor in deciding which crops are to be tried or sustained, or whether agriculture can compete with the pulpwood industry. For world or national planners, photosynthesis might be decisive. Such thinkers would perhaps judge that the best crops to pursue in Nova Scotia would be blueberries or balsam fir trees. Some of our other crops like corn are at the northern limits of their range and do not compete with those of sunnier zones. However, the sun's efficiency declines in relative importance as provincial and local interests intrude on those of national planners. Socio-economic factors take over, such as keeping people at work on the land, feeding ourselves, supplying fodder for our stock rather than relying on imports, and generally maintaining agriculture as a going concern. Later studies will be needed to compare the scientific interpretation of efficiencies of individual crops with economic and political imperatives.

Table IX. Agricultural commodity balance sheet, expressed as percentages, Nova Scotia 1973. For absolute values see Tables X and XI of Appendix.

		Relative Nova Scotian production (total per section equals 100)	Percent of required commodity imported from outside Nova Scotia
I	CROPS	Based on areas	
	Hay (60,000 hectares) Silage corn (5,000)	74.6	-
	Potatoes (1.500)	1.7	71
	Vegetables (725)	0.8	67
	Grain (15,000)	17.0	80
	Fruit trees (5,000)	5.6	-
	Strawberries (275)	0.3	40
II	ANIMALS	Based on edible yields	
	Pork	26	63
	Beef and veal	29	73
	Mutton & lamb	1	66
	Chicken & turkey	44	17
III	DAIRY PRODUCTS		
	Fluid milk	70	0
	Butter, cheese, etc. calculated as fluid milk equivalents.	30	72

Possibilities for Import Reduction

On the product side, Nova Scotia is a net importing agricultural area (Table IX). The only commodities which are exported outside the province are eggs (10%), blueberries (90%), and apples (50%). Nova Scotia produces only 40% of the food consumed by its small population (Fig 1), a quantity which is clearly too small to influence product prices throughout North America. Hence, prices are set externally, and Nova Scotian producers must meet the production plus transportation costs from other areas in order to retain local markets. Any proposed energy alternatives must take into account the already low Nova Scotian farm incomes. The imposition of higher dollar production costs to facilitate energy savings may be unacceptable in the short run.

Imports, of course, are of numerous classes:

— There are goods from warmer climates such as coffee or oranges or prepared fruit and condiments, a class which does not merit further consideration here.

— There are many of our own summer products brought to us out of season, to which we have become accustomed, and any loss of which we shall accept only under economic stress. There is the beginning of local alleviation of potential shortage by a minor development of greenhouses near sources of waste heat, but it is still mostly only in the talking stage and offers a fruitful field for technology.

— There are products formerly local but now imported from elsewhere in Canada, notably food imports which make up half the farm inputs shown in Figure 1 and which are heavily subsidized. Most of our meat comes from outside, as does nearly all the flour for our bread. In pioneer times, the oatmeal for our food was locally produced and it is today a product much favoured by health enthusiasts. Probably effective advertising, coupled with rising wheat costs, could restore oatmeal to a more prominent position.

— Finally, there are so-called imports which circulate within our own region of the Maritimes and Quebec. Whether these should be called imports in the sense of the classes listed above is a political question related to the degree of provincialism prevalent in our area and subject to discussion in The Atlantic Provinces Economic Council (APEC).

We have not seen published figures with which to quantify the foregoing list, which indicates a large field for research into the ways in which the energy situation will affect economic decisions about imports. The increasing energy shortages will allow new methods for agricultural products to become viable. For instance, transport costs from California will, as they increase, allow local farm costs to become competitive. To cite an example: the largest Nova Scotian foreign import (by weight) is lettuce which increased by 30% between 1973 and 1978. During the same period the local product (by hectarage) declined to the same degree (Nova Scotia Agricultural Statistics 1978). Another example is feed imports which account for one-half the animal requirements, and which could be grown locally if economic considerations so dictated.

Support Programs

The rise of government-sanctioned marketing boards has paralleled the rise of capital-intensive agriculture. Unquestionably, the attainment of a stabilized level of prices and production in important commodities such as milk, eggs, and poultry, has important effects throughout the agricultural sector. Just what the implications of these effects are for energy utilization remains to be clarified. For example, do marketing boards, by ensuring a given level of production, encourage investment in energy-intensive methods and, by perpetuating the status quo, encourage energy inefficiency? If more energy-efficient crops can be discovered, how is the farmer to be induced to grow these crops and the consumer encouraged to buy them?

In Nova Scotia, the agricultural industry also receives subsidies and grants from provincial and federal sources. The Nova Scotia Department of Agriculture's financial assistance to the farmers is largely in the form of capital grants rather than operating grants. Exceptions to this general direction would be the provincial Agricultural Limestone Assistance Policy ($850,000 in 1979) and the federal Feed-Freight Assistance Policy (currently almost $2 million annually).

A major thrust of government-funded support programs is to encourage the development and modernization of farm units and where possible encourage the adoption of new or improved technology. Most of the policies fall into 1 of 3 general categories: (1) land improvement, (2) feed grain and protein crop production, and (3) livestock policies designed to lessen Nova Scotia's dependence on imported meat. Increased energy costs involved in promoting all 3 could be very significant. Typical policies of this nature would be the Fertilizer Assistance Program, the Capital Grants Policy and the Land Improvement Policy (Agriculture Assistance Program).

Eligibility for many of these support programs depends on a commitment of the farmer, who must gross $10,000 or more per year to qualify.

The jointly funded Agricultural Development Agreement policies have the objective of increasing the province's agricultural production. These programs operate on a cost-share basis with 20% of the costs from the Province and the remainder from the Federal government.

The total dollar value of grants and other forms of economic assistance paid to Nova Scotia agriculture in 1975-1976 was $7.2 million, which was some 5% of the gross value for agricultural production in the province.

Little available information exists concerning the effects which the grants and subsidies offered to local farmers have had on agricultural patterns in Nova Scotia. Consequently, the long-term impacts, including ecological and socio-economic, of government economic support programs on agricultural trends in Nova Scotia are presently unknown. The short-term impact appears to be the perpetuation of an energy-intensive and capital-intensive status quo. None of the financial incentives in force at present has the object of persuading farmers to alter their patterns of energy consumption. An offer of incentives could reduce the costs and risks of investment in energy-saving equipment and techniques. Information transfer programs, demonstrations, and technical assistance would be a natural accompaniment to financial aid.

Possible sources of energy savings must take into account the size, diversity, and scale of production units. Other strong imprints on our agricultural industry are made by the marketing boards, which tend to perpetuate the status quo, and by provincial and federal support programs with the intent of introducing new technology. None of the financial incentives in force at the present time has the object of reducing the costs and risks of investment in energy-saving equipment and techniques, which might be accompanied by technical assistance.

We people of the West can get back 25% of what plants cost us as food energy. Animal food yields us only 10% of the input energy. It is not surprising, therefore, that the contemporary world scarcity is especially related to animal protein and that the special effort of the times is to seek more protein from plants.

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Appendices

A. *Detailed Source Tables*

This section gives the primary source tables which have been summed up as Tables V and VI. Table X is concerned with the plants destined for human consumption and Table XI with animal products. The source is Nova Scotia Agricultural Statistics (1975) and the entries represent 5-year averages from 1971-1975. The first entry is the annual Nova Scotian edible yield (column 1) as millions of kilograms. Sometimes column 1 is a multiple of rate of yield and area under cultivation, sometimes a direct value, and it may originate as bushels, quarts or tons. Some numbers are from general sources recalculated or extrapolated to make them applicable to Nova Scotia. Bracketed numbers are assumed by analogy.

Reference sources for columns 2 and 4 which give unit input and output costs are given in the text. From them come the final annual totals for Nova Scotia in columns 3 and 5 which lead to the easily compared percentage numbers of column 6.

The notes on individual crops are intended to be self-explanatory and the gaps and assumptions shown will enable a reader to form a personal estimate of the probable level of accuracy.

Table X. Detailed relations of plants destined for human consumption, from direct observations. Annual yields are 1971-1975 averages from Nova Scotia Agriculture Statistics (1975).

INDIVIDUAL OBSERVATIONS	1 Annual N.S. edible yield (kg x 10^6)	2 Input (kcal/kg of edible product)	3 Annual N.S. input (kcal x 10^9) (1 x 2)	4 Food value (kcal/kg) (Table XII)	5 Annual total for N.S. (kcal/ x 10^9) (1 x 4)	6 Food energy as % of input energy
I. ON THE FARM						
Wheat. 36 bu/acre x 68 gives kg/ha	3.6	547	2.1	Dried 4200	15.1	720
VEGETABLES						
Potatoes	27.0	752	20.3	850	23.0	112
Carrots	11.7	463	5.5	420	4.9	89
Remainder as detailed below.	6.5	606	4.0	380	2.5	63
Beans. Col. 1 was reported dried as 0.1, converted to fresh as 1.0. Col. 4. was similarly changed from 3400 dried to 340 fresh.	1.0			340	0.3	

Cabbage	2.6			240	0.6	
Corn	1.0			960	0.9	
Tomatoes	0.6			220	0.2	
Other: beets, cauliflower, cucumbers, lettuce, parsnips, total.	1.3			363	0.5	
TOTAL VEGETABLES	45.2		29.8		30.4	100
FRUITS						
Fruit trees						
Apples. One bushel taken as 18 kg. Fresh sales make up 35% of crop.	41.6	516	21.6	580	24.1	110
Blueberries	4.1	(331)	1.4	680	2.8	200
Strawberries	0.8		0.6	410	0.3	
Information insufficient for residual fruit calc. Say	(0.5)	(440)		250	1.0	(150)
Total fruit	47.0		23.6		28.2	119
GRAND ON-FARM TOTAL	95.8		55.5		73.7	135

II. POST-FARM. Processing, commercial handling including transportation, and home preparation. (After Whittlesay & Lee 1976; cited from Agriculture Canada 1977, Tables 32 *et seq.*)

Wheat (col. 4 at 4200): proc. 2.0; com. hand. 0.7; home 3.5.			6.2		15.2	245
Potatoes (assume 1/2 fresh and 1/2 prepared): proc. 72.5; com. hand. 43.7; home 54.4.			170.6		23.2	14
Carrots (assume all fresh): proc. nil; com. hand. 13.8; home 21.5.			35.3		5.0	14
Other vegetables (assume fresh & av. of other veg.): proc. nil; com. hand. 10.0; home 15.6.			25.6		2.5	10
Apples (N.S. Agric. Stat. give 65% processed & 35% fresh): proc. 4.6; com. hand. 30.1; home 9.2.			43.9		24.3	56

Blueberries (assume canned & same as green peas. Assume food value same as bilberries): proc. 3.6; com. hand. 2.3; home 2.2.			8.1		2.8	35
Other fruit (assume fresh & same prep. costs as for vegs.): proc. nil; com. hand. 1.5; home 2.3.			3.8		0.9	24
TOTAL			293.5		73.9	25
GRAND TOTAL, PLANT FOOD			349.0		73.8	21

Table XI. Detailed relations for livestock, dairy products, poultry and eggs. (Nova Scotia Agricultural Statistics 1975, 1978.)

INDIVIDUAL OBSERVATIONS	1 Annual edible yield (kg x 10^6)	2 Input (kcal/kg of edible product)	3 Annual input (kcal x 10^9) (1 x 2)	4 Food value (Kcal/kg)	5 Food value annual N.S. total (kcal x 10^9) (1x4)	6 Food energy as % of input energy (100 col. 5/col. 3)
I. ON THE FARM						
FODDER						
Pasture	190.8	192	36.7	2400	458.0	1250
Hay	267.3	335	89.5	2400	651.5	728
Corn for silage. Ann. yield increasing; av. for '75 & '76 taken.	127.3	220	28.0	812	104.1	372
TOTAL			154.2		1213.6	787
GRAINS						
Barley. 39 bu/acre x 56 gives kg/ha.	4.8	(556)	2.7	Dried 4200	20.1	753
Mixed Grain. 44 bu/acre x 49 gives kg/ha.	6.4	(556)	3.5	4200	26.9	751

Oats. 44 bu/acre x 49 (est.) gives kg/ha.	17.9	(556)	10.0	4200	75.1	754
TOTAL	29.1	(556)	16.2	4200	122.1	754
IMPORTED FEED (as on chart)			766.0			
TOTAL ON-FARM FEED & FODDER			936.4		1335.7	143
II. PROCESSING & HANDLING						
BEEF						
Cattle production from Statistics Canada, probably omits local use.	1.94					
Alternate N.S. Dept. Agriculture Statistics. More probable. Accepted beef, 94%; veal, 6%; total 59,000. Cattle av. 132 kg usable yield.	7.79	23,000	179.1	3,000	23.4	13
HOGS						
N.S. Agric. Stat. (1975) annual numbers are 110,000 each with 63 kg usable yield. Statistics Canada figures are in agreement.	7.00	16,500	116.0	4,000	28.0	24
TOTAL LIVESTOCK			295.1		51.5	17
POULTRY						
Production in N.S., 5-yr average. Dressed weight of fowl, chicken, turkey, geese and ducks.	12.2	18,000				
Broiler output.				1,500		
Suggested ratio. Back calculation.			(220.0)		(18.3)	8

(Some Geigy values)						
Broilers				1,110		
Raw Chicken				1,790		
Duck				3,210		
Goose				3,490		
Turkey				2,620		
EGGS						
Production in N.S., 5-yr average. Dozens.	1.3			1,580	2.0	
Suggested ratio. Back calculation.		(9,200)	(12.0)			17
TOTAL POULTRY PRODUCTS			232.0		20.3	9
DAIRY PRODUCTS						
Total milk. 5-yr average is 160 x 10^6 kg of which 95% is consumable.	152.1	1,270	194.7	650	99.7	51
ADDED COSTS TO PROCESS MILK PRODUCTS. Milk equivalents, 18% for butter.	27.0	7,190	10.0	7,160	10.0	100
17% for other factory products, dehydrated milk, cheese, ice cream. No breakdown available.	26.0	(1,270)	33.0	650	27.2	82
TOTAL DAIRY PRODUCTS			237.7		99.7	42
TOTAL PROCESSING & HANDLING			764.8		171.4	22
GRAND TOTAL ANIMAL FOOD FOR HUMANS			1701.2		171.4	10

B. *Constancy of Energy in Dried Fruits and Vegetables*

When calorific values are stated for fresh food products there is a wide variability; thus cucumbers, lettuce and pumpkins average 140, while corn, parsnips and potatoes average about 850 kcal/kg (Table XII). When products are dried a good deal of the difference disappears; the first three products mentioned average 1336, the second group 1712, so that the 6-fold difference in the fresh vegetables is reduced to a 28% difference when they are dried. The so-called "local" values were the ones used in our own calculations and came from several reference sources. They differ little from the Geigy numbers and probably have the same real variability depending on the time of harvesting and kind of season.

The mean calorific value for the 15 Geigy vegetables was 1533, while for the three fruits it was 1785. The number of fruits is too small to say whether the difference is real.

As regards water content, most fresh fruits and vegetables have 80-90% while commercially dried beans and peas have 5-10%. We do not have a water content figure for dried grains.

Table XII. Comparison of energy ratings of commercial products with those for totally dried products. General source is the Geigy tables (1956). "Local" items as used in our calculations had several sources. There are also some numbers from Stutt (1973). All figures are in kcal/kg.

	Commercial product	Totally dried product
DRIED GRAINS (Stutt 1973)		
Soybeans	4700	
Sunflower seed	4500	
Wheat, oats, barley, corn	4170	
DRIED VEGETABLES		
Haricot beans	3510	3690
Local beans	3400	3574
Peas	3540	3934
FRESH VEGETABLES		
Green beans	351	3217
Beets	331	2668
Cabbage	249	3038
Local cabbage	240	2930
Carrots	400	3502
Local carrots	420	3676
Cauliflower	311	3746
Fodder corn (Stutt 1973)	1151	
Local corn	961	3846
Local silage corn	221	3380
Cucumber	130	2957
Lettuce	150	2884

Parsnip	781	3647
Peas	800	3202
Potatoes (Stutt 1973)	944	
Potatoes	851	3834
Local potatoes	759	3418
Pumpkins	150	2999
Tomatoes	230	3887
Local tomatoes	221	3737
Turnips	320	3513
FRUIT		
Apples	580	3616
Bilberries (like blueberries)	679	4090
Strawberries	410	4100

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THE LOCAL OCCURRENCE OF AGARUM CRIBROSUM IN RELATION TO THE PRESENCE OR ABSENCE OF ITS COMPETITORS AND PREDATORS

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In a sublittoral survey of 6 sites on the Atlantic and Fundy shores of Nova Scotia, 3 main types of community structure were found. In the first, *Agarum cribrosum* occurred in association with 2 *Laminaria* species (competitors) and sea urchins (predators). In the other 2 types, *A. cribrosum* was absent where either (a) the competitor or (b) the predator occurred, but not both.

Introduction

The occurrence of sublittoral seaweed zones in Nova Scotia has been reported by Edelstein et al. (1969) and Mann (1972). Commonly a *Laminaria* zone dominates the shallow sublittoral with *Agarum cribrosum* forming nearly homogeneous stands in deeper water. A similar distribution has been reported by Vadas (1968) for the northeastern Pacific. Vadas showed experimentally that the absence of an *Agarum* population in shallow water is a result of interspecific competition with other laminarian species. The development of a deep-water *Agarum* zone was shown to result from the selective grazing of sea urchins which are attracted to kelp species other than Agarum.

As will be shown, the development of a deep-water *Agarum* population and a shallow-water *Laminaria* population as described by Edelstein et al. (1969), Mann (1972) and Vadas (1968) is typical of only 1 class of shore in Nova Scotia. *Agarum* is absent from 2 other types of shore depending on the presence or absence of *Laminaria* species and/or sea urchins. We report here on the results of a survey of 6 sites on the Atlantic and Fundy shores of Nova Scotia. These data are compared with the experimental analyses of Vadas (1968).

Methods

The survey was done in July and August 1979. The 6 sites chosen are shown in Figure 1. Dramatic changes in the sublittoral community structure have occurred in St. Margaret's Bay, Nova Scotia (Mann 1977). We therefore attempted to choose sites not obviously undergoing gross biotic changes. Observations at 4 of the sites over many years have shown minimal changes.

At each of the sites a transect line was run perpendicular to the shore out into the sublittoral zone. Quadrats (0.5 m x 0.5 m) were cleared of all kelp species (if present) at various depths along the transect. Sea urchins were recorded as present or absent at each site. The kelps collected in each quadrat were recorded and weighed by species.

Water transparency was measured at each site with a Secchi disc.

Results

The biomass distribution of kelps by species is shown in Table I. One or more species occurred in each of 5 sites. No kelps were found at Mill Cove where sea urchins (*Strongylocentrotus droebachiensis*) dominated the benthos. Sea urchins were

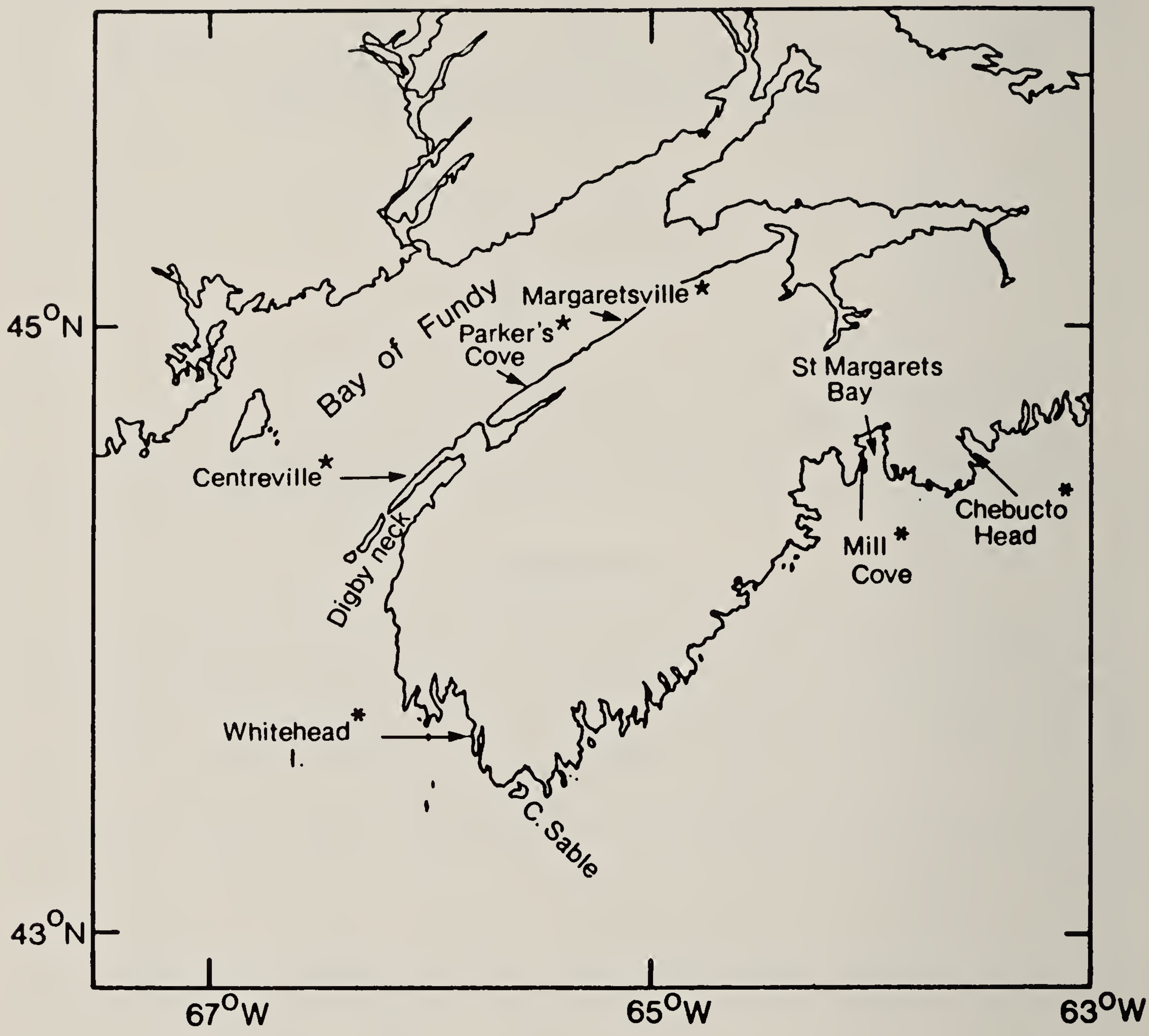

Fig 1. Study site location. Sites examined are marked with an asterisk.

present at all sites except Whitehead Island off the Pubnico peninsula. *Agarum* was found only at sites where both sea urchins and *Laminaria* species were present. At Whitehead Island, where both sea urchins and *Agarum* were absent, *Laminaria* species penetrated into depths at which *Agarum* populations are normally found.

Water turbidity and tidal amplitude were greatest in the Bay of Fundy sites (Table II).

Discussion

Vadas (1968) discussed the depth distribution of *Agarum* at sites where both sea urchins and other kelp species were present. This type of benthic structure is only 1 among 3 found in our survey of southern Nova Scotian shores. The other types found were (1) shores with sea-urchins, without *Agarum* and without other kelp species, and (2) shores with *Laminaria* species, but without *Agarum* and without sea urchins. The existence of community structures other than that described by Vadas (1968) does not detract from his view that the occurrence of deep-water *Agarum*

Table I. Fresh mass (g) of 4 kelp species in 0.25-m^2 quadrats by depth at 5 sites. Depths are in metres below chart datum.

Depth (m)	*Alaria esculenta*	*Agarum cribrosum*	*L. longicruris*	*L. digitata*
		CHEBUCTO HEAD (+ sea urchins)		
22	0	364	0	0
20	0	208	0	0
17.5	0	102	0	0
14.5	0	70	0	0
12.5	0	85	0	0
11.5	0	40	0	0
8.5	0	0	152	129
7	0	0	25	327
5.5	77	0	35	292
1.5	96	0	333	207
0	0	0	0	0
		WHITEHEAD ISLAND (No sea urchins)		
18	0	0	0	0
16	0	0	468	23
14.5	0	0	133.5	81.5
13	0	0	123.5	117.5
11.5	0	0	0	2
10	0	0	353.5	677.5
7.8	0	0	0	760
6.5	0	0	368.5	590
4.5	0	0	1652.5	112.5
1.5	0	0	0	1410
0.8	0	0	827.5	0
		CENTREVILLE (+ sea urchins)		
11	0	88	0	0
8.5	0	101.5	0	0
7.5	0	138.5	0	0
6	0	181	0	0
5	0	122.8	0	0

Depth (m)	*Alaria esculenta*	*Agarum criborsum*	*L. lonicruris*	*L. digitata*
3.3	0	0	0	0
3	0	0	0	1498
0	0	0	0	1602
+0.5	1013	0	0	458.5
+0.8	275	0	0	446.5
+1.0	0	0	0	0
PARKER'S COVE (+ sea urchins)				
4.8	0	0	0	0
4.3	0	0	0	0
3	0	0	0	0
2.2	0	0	0	0
1	0	0	0	0
0.5	0	0	0	194
+0.1	80	0	0	0
+1.0	0	0	0	0
MARGARETSVILLE (+ sea urchins)				
5	0	0	0	0
3.5	0	10	0	0
3	0	8	110	0
1.6	0	0	530	0
0.7	0	0	735	0
0.4	0	0	0	458
+0.2	0	0	0	0

Table II. Secchi transparencies and large tide amplitudes at 5 sites.

Site	Secchi transparency (m)	Tidal amplitude[1] (m)
Chebucto Head	> 7.5	2.1
Whitehead I.	3.3	4.2
Centreville	4.2	8.2
Parker's Cove	2.75	9.8
Margaretsville	1.06	11.5

[1] From Fisheries and Environment Canada (1979)

beds depends on the predatory activities of sea urchins, and on the competitive interactions of other kelp species. On the contrary, our data lend weight to the thesis of Vadas. The biological variation among the shores of Nova Scotia provides a "natural" experiment in the sense of Estes et al. (1978). Among the classes of community structure examined we found that *Agarum* occurred only in sites where both its predator (sea urchins) and competitive superior (*Laminaria*) were present together. Where only either the predator or competitor, but not both, were found, *Agarum* was absent. At Whitehead Island, where sea urchins were absent, *Laminaria* populations penetrated to 16 m depth. Presumably members of this genus are able to out-compete *Agarum* in its usual depth range in the absence of selective grazing by sea urchins.

Where *Laminaria* is absent, *Agarum* is destructively grazed by sea urchins. This is known with certainty for Fox Point in St. Margaret's Bay where we have observed the destruction of a mixed kelp forest by urchin grazing. *Laminaria* species were destroyed first, leaving *Agarum* as the only surviving kelp species. *Agarum* was finally consumed, leaving barren grounds dominated by sea urchins and encrusting coralline algae.

During conversion of a kelp forest to sea urchin-dominated barrens, *Agarum* can thus be found as the only kelp species present with sea urchins. However, this combination occurs only briefly during a period of disequilibrium. Under periods of equilibrium, *Agarum* is not expected to occur as the only kelp species associated with sea urchins.

Parker's Cove, a site in the Bay of Fundy, requires separate consideration. Here *Agarum* would have been expected as a member of the benthos, given that sea urchins and *Laminaria* were present. The absence of *Agarum* is related to the small-scale structure of the shore community. Below 0.5 m depth, macro-algae were absent from the sea urchin-dominated barrens. In the wave-swept intertidal fringe urchins were absent. Here a narrow refugium dominated by *Alaria esculenta* and *Laminaria digitata* was found. Narrow refuges from sea urchin grazing are common on wave-swept shores of Nova Scotia. Semi-sheltered sites are commonly grazed into the intertidal and are thus free of kelp (e.g. Mill Cove in this study).

The variations in biological interaction among the sites considered here are manifested, in part, by the presence or absence of *Agarum*. The sites also varied in their abiotic characteristics, notably exposure to surf action, tidal amplitude, and water transparency. All of these differences are related to some of the data variation between sites shown in Table I. For example, *Alaria esculenta* was found only in sites exposed to strong wave action. Similarly, the lower depth limits of each of the kelp species were quite different at Chebucto Head, a site with clear water and small tidal amplitude, than at Margaretsville, a site with turbid water and large tidal amplitude (Table II). It is necessary to be cognizant of the importance of these abiotic effects when attempting to interpret the results of biological interaction.

Acknowledgements

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RESPONSES OF THE OSTRICH FERN, MATTEUCCIA STRUTHIOPTERIS (L.) TODARO, TO LIME, SOIL MOISTURE, AND IRRADIANCE

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Mature sporophytes of *Matteuccia struthiopteris* were grown in controlled environment chambers at 3 lime [$Ca(OH)_2$] levels, 2 soil moisture levels, and 2 irradiance levels. The effects of these treatments on vegetative and fertile frond fresh and dry weights, frond height and frond nutrient concentrations were measured. Soil moisture had the greatest effect and was the only variable affecting frond weight. Increased irradiance reduced frond height but increased the number of plants producing a second set of fronds. Liming had no effect on frond weight, number, or height. It interacted with soil moisture and irradiance in their effect on frond nutrient concentrations. Fertile fronds had a nutrient depletion effect on the vegetative fronds and higher concentrations of nitrogen, phosphorus, and potassium than vegetative fronds. Calcium levels in the fertile and vegetative fronds were unaffected by any of the variables. The association of *M. struthiopteris* with calcareous soil may be due to the soil's effect on another stage in the fern's life cycle, such as spore germination, gametophyte growth, or fertilization.

Introduction

The ostrich fern, *Matteuccia struthiopteris* (L.) Todaro [=*Pteretis pensylvanica* (Willd.) Fern.] is widely distributed in temperate North America and Eurasia (Lloyd 1971). In North America it is sometimes designated var. *pensylvanica* (Willd.) Morton because of the larger stature and uniformly brown scales on the frond stipe. *M. struthiopteris* is dimorphic, producing sterile photosynthetic fronds early in the spring, followed 1 to 2 months later by fertile, nonphotosynthetic fronds on some of the plants.

M. struthiopteris is most commonly found in shady habitats on or near river flood plains where the soil is moist and high in nutrients (Mueller-Dombois 1964; Porfir'ev 1975). There are also reports that it occurs only on calcareous soils. It is absent from the noncalcareous Atlantic coast of Nova Scotia (Roland & Smith 1969) and the eastern half of Newfoundland. Several reports indicate the greatest abundance of ostrich fern on limestone soils and gypsum outcrops (Chrysler & Edwards 1947; Fernald 1921; Roland & Smith 1969). However, both naturally occurring and transplanted plants have been observed growing on sites of acid pH, under conditions of full sunlight and/or low moisture (Gabrielson 1964; R.K. Prange, unpubl.).

Although *M. struthiopteris* is generally not regarded as a food plant, the Maliseet Indians of the Penobscot and Saint John River Valleys of Maine and New Brunswick have traditionally utilized the "fiddleheads" (young vegetative fronds) as a spring vegetable. Since the United Empire Loyalists first settled in the region the taste for "fiddleheads" has grown considerably and today the annual commercial harvest of "fiddleheads", obtained entirely from wild populations, is estimated to be 225,000 kg. The demand for this vegetable has exceeded the supply and there is an obvious need to domesticate and cultivate *M. struthiopteris.* In order to do this a greater understanding of its responses to environmental variables must be known. It is especially important to understand the nature of the requirement for soil moisture, irradiance and calcium. This experiment examines the response of the ostrich fern to these variables under controlled environment conditions.

Methods

Forty-eight dormant plants of *M. struthiopteris* were collected in early May from a population growing on the grounds of the Nova Scotia Agricultural College, Truro, Nova Scotia. These were grown for 45 days in controlled environment chambers at 3 lime, 2 soil moisture, and 2 irradiance levels with 4 replicates (plants) of each treatment.

Each plant was planted in a pot 25 cm in diameter containing sterilized greenhouse soil composed of 62% compost, 25% peat moss, 13% sand by volume, with 250 ppm 20% superphosphate. To determine the effect of calcium, 3 levels of $Ca(OH)_2$ were applied: (a) 0 g kg^{-1} of soil; (b) 2 g kg^{-1}; and (c) 4 g kg^{-1}. The pH of each lime treatment was recorded at the beginning, after 27 days and at the end of the experiment (45 days).

Within each lime treatment, 2 levels of plant water stress were applied by controlling soil moisture. A condition of low water stress (high soil moisture) was obtained by maintaining the soil moisture near 100% field capacity by applying distilled water daily until it dripped out the bottom of the pots. A condition of high water stress (low soil moisture) was provided by reduced watering. Daily measurements of the soil were made with a JLM soil moisture probe and the plants were not watered until the moisture probe reading dropped to the 30-40% value between field capacity and permanent wilting point, when water was applied slowly until the level reached 50-60%. Six soil samples were taken from the pots and measured on a pressure plate. At tensions of 30 kPa (field capacity) and 1500 kPa (permanent wilting point) the soil moisture was 20.7% and 11.5% of the dry weight, respectively.

The plants were grown in 2 Conviron walk-in controlled environment chambers, both set at 20°C, 70-80% relative humidity, and 16:8 h light:dark photo-period. Light was supplied by 40-W incandescent bulbs (25% input wattage) and 110- and 215-W cool-white fluorescent lamps (75% input wattage), 1.16 m above the tops of the pots. The irradiance, as measured by a Li-Cor LI-185A quantum meter O.65 m below the lights, was 160 μmol m^2s^{-1} in the low irradiance chamber and 418 μmol $m^{-2}s^{-1}$ in the high irradiance chamber.

Throughout the course of the experiment, 1 vegetative frond from each plant was regularly measured for total height by pulling the frond to its maximum length along a meter stick. At the end of the experiment, the heights of all the fronds were recorded. The fronds were harvested and, following fresh and dry weight determination (55°C for 72 h), were analyzed by the Soils and Crops Laboratory, Nova Scotia Department of Agriculture and Marketing, for percent nitrogen, calcium, magnesium, potassium and phosphorus.

During the experiment vegetative fronds appeared on all the plants and near the end of the experiment some plants also produced fertile fronds. These fertile fronds were analyzed separately for dry and fresh weights and foliar nutrient concentrations.

After harvesting, the plants were kept in the controlled environment for 4 weeks to determine the effects of the experiment on subsequent production of fronds. During this period, all of the pots were watered to field capacity, leaving only 2 variables, irradiance and lime.

The results were examined statistically using a 1-, 2-, and 3-way analysis of variance (ANOVA). Standard errors (SE) were included for data that were not significant in the ANOVA or not subjected to a statistical test.

Table I. Significant levels of F^1 for effects of liming, soil moisture and irradiance on frond weight, number, height, and mineral composition.

		Fresh weight		Dry weight			Vegetative fronds					
Source	df[2]	Total	Fertile	Total	Fertile	Fronds/ plant	Height	N %	K %	P %	Mg %	Ca %
Irradiance (I)	1	NS	NS	NS	NS	NS	**	**	**	**	NS	NS
Lime (L)	2	NS	NS	NS	NS	NS	NS	NS	NS	NS	**	NS
Moisture (M)	1	**	*	**	*	NS	**	**	**	*	NS	NS
I x L	2	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	NS
I x M	1	NS	NS	NS	NS	NS	**	NS	*	NS	NS	NS
L x M	2	NS	NS	NS	NS	NS	NS	**	**	*	NS	NS
I x L x M	2	NS	NS	NS	NS	NS	NS	NS	**	NS	NS	NS
Error	36											
Total	47											

1 — Variance ratio test for homogeneity of means
2 — Degrees of freedom

NS — Not significant at 5% level.
* — Significant at 5% level.
** — Significant at 1% level.

Results

Soil pH levels during the experiment varied little within each lime treatment. The soil pH's (±SE) for the lowest to highest lime levels were 5.1±0.2, 6.5±0.1 and 7.4±0.1, respectively. Since liming had an effect on soil pH but no significant effect on calcium levels in the fronds (Table I), the significant effects of liming noted In Table I could really be due to changes in soil pH.

The fresh and dry weights of both the vegetative and fertile fronds were significantly affected by the soil moisture level (Table I; Fig 1). High soil moisture, compared to low soil moisture, increased fresh and dry weights of vegetative fronds by 47% and 70% respectively and of fertile fronds by 461% and 510% respectively.

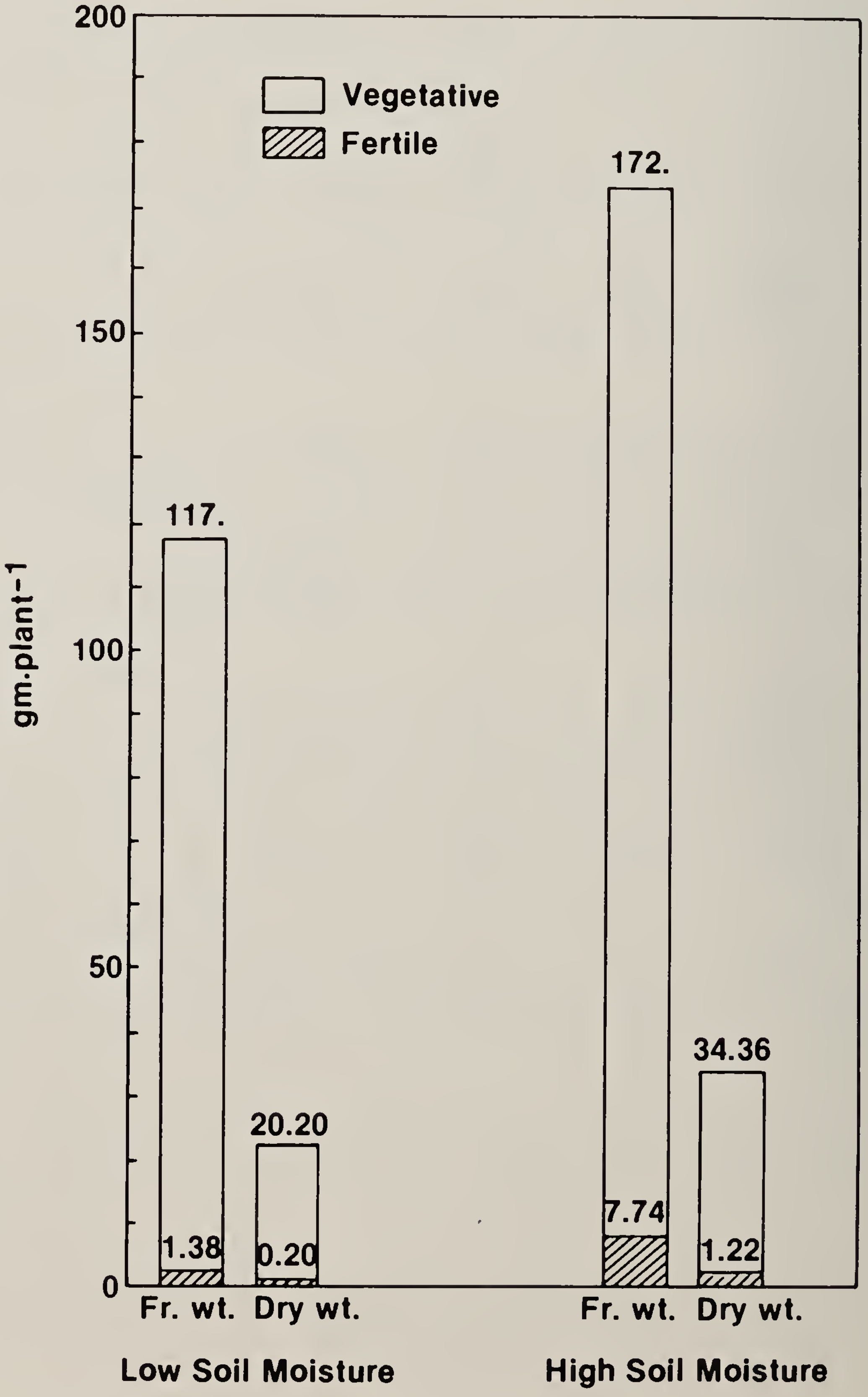

Fig 1. Effect of soil moisture on frond production (fresh and dry weights)

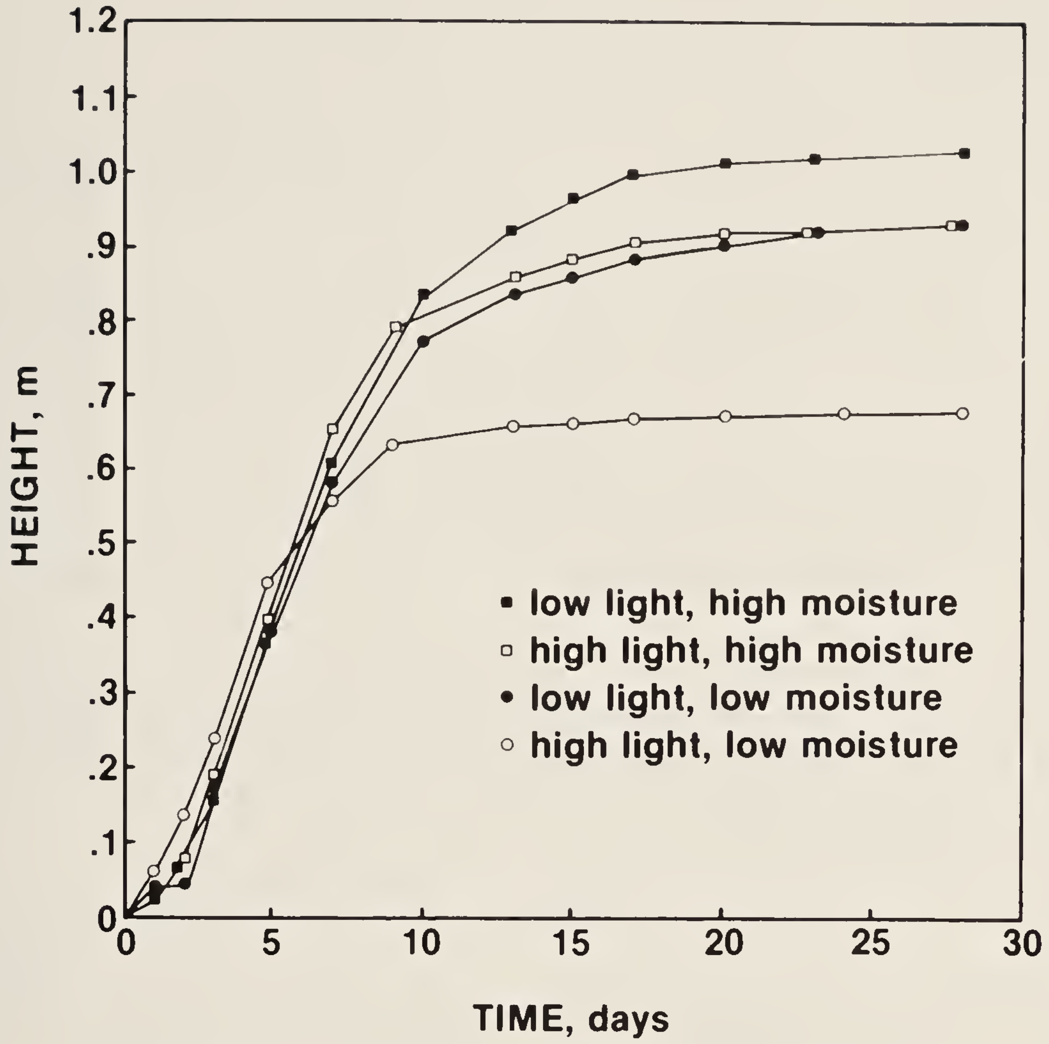

Fig 2. Effect of soil moisture and irradiance on frond height. High light = 418 μmol $m^{-2}s^{-1}$; low light = 160 μmol $m^{-2}s^{-1}$.

Both soil moisture and irradiance significantly affected frond height (Table I). Increasing soil moisture increased the height, whereas increasing irradiance decreased height by almost the same amount (Fig 2). In the first 5 days after germination, high irradiance combined with low moisture produced the greatest rate of frond elongation but after 5 days the fronds had completely opened, increasing the surface area for transpiration. This treatment had the slowest rate of elongation for the remainder of the experiment. Fronds in the high irradiance treatments developed more brown tips than in the low irradiance treatments.

Changes in fresh and dry weights were not due to changes in number of fronds produced (Table I). The number of fronds per plant was not significantly different in any of the treatments (Mean±SE = 6.40±0.33 fronds/plant).

The percent nitrogen in the vegetative fronds was less at the high irradiance (Table II). Lime and soil moisture treatments interacted (Table III). At the high soil moisture level, concentrations of nitrogen and phosphorus dropped with lime level and at the low soil moisture level they increased. The low soil moisture level had a higher mean value (1.95%) for nitrogen than the high soil moisture level (1.45%).

The ANOVA of the percent potassium concentrations in the vegetative fronds indicated a significant 3-way interaction among the irradiance, lime, and soil moisture treatments (Tables I, IV). This 3-way interaction can be seen by examining the responses of potassium concentration at the 2 g kg^{-1} lime level in Table IV. At this lime level the low soil moisture plants had their lowest potassium concentration and the high soil moisture plants had their highest potassium concentration. This interaction of lime and soil moisture was more noticeable at the high irradiance level than the low irradiance level.

Table II. Effect of irradiance on percent nitrogen and phosphorus in vegetative fronds.

	Irradiance (μmol $m^{-2}s^{-1}$)	
	160	418
Nitrogen (%)	1.89	1.52
Phosphorus (%)	.28	.22

Table III. Effect of interaction between soil moisture and liming on percent nitrogen and phosphorus in vegetative fronds.

	Soil Moisture			
	Low		High	
Lime (g kg^{-1})	N (%)	P (%)	N (%)	P (%)
0	1.66	.25	1.52	.24
2	2.07	.26	1.48	.27
4	2.12	.30	1.36	.18

Table IV. Effects of liming, soil moisture and irradiance on percent potassium in vegetative fronds.

	Irradiance (μmol $m^{-2}s^{-1}$)					
	160			418		
Soil	Lime (g kg^{-1})			Lime (g kg^{-1})		
Moisture	0	2	4	0	2	4
low	1.54	1.18	1.74	1.17	.90	1.63
high	1.31	1.32	1.20	.96	1.58	.88

The percent phosphorus in the vegetative fronds had a similar pattern to percent nitrogen. That is, increased irradiance decreased the phosphorus concentration (Table II) and liming and soil moisture interacted on phosphorus concentrations (Table III). In the lime X moisture interaction, the values were similar at 0 g kg^{-1} and 2 g kg^{-1} between moisture levels. However, at 4 g kg^{-1} the phosphorus concentration was most affected by soil moisture, with the highest phosphorus concentration at the low soil moisture level and the lowest at the high soil moisture level.

Even though the lime levels were established by $Ca(OH)_2$, the percent calcium concentration in the vegetative fronds was not significantly affected. The mean calcium concentration (± SE) was 1.14 ± 0.04%.

The percent magnesium in fronds was significantly affected by an interaction between irradiance and lime (Tables I, V). At the high irradiance level, the magnesium concentration was greatest at lime treatment 0 g kg^{-1}, whereas plants grown at low irradiance had high magnesium concentrations at lime treatments 0 and 4 g kg^{-1}.

Table V. Effect of interaction between irradiance and liming on percent magnesium in vegetative fronds.

Lime (g kg^{-1})	Irradiance (μmol $m^{-2}s^{-1}$) 160	418
0	.18	.22
2	.15	.15
4	.18	.15

A comparison of vegetative fronds from infertile plants, vegetative fronds from fertile plants, and fertile fronds (Table VI) showed that plants that produced fertile fronds had greater fresh and dry weight of vegetative fronds than did infertile plants. The presence of fertile fronds also decreased the concentration of nitrogen, potassium, and phosphorus in the vegetative fronds on the same plant. Calcium and magnesium concentrations in the vegetative fronds remained the same, regardless of the presence of fertile fronds. Compared with vegetative fronds, fertile fronds had higher concentrations of nitrogen, potassium, and phosphorus; magnesium was similar; and calcium was considerably lower.

After the fronds were harvested and the plants were watered to the high soil moisture level, fronds appeared on some of the original plants and also from new plants (Table VII). The total number of plants producing a second set of fronds was substantially greater in high irradiance (n=30) than in low irradiance (n=10). Although not recorded, the number of fronds per plant was fewer than in the first set.

Discussion

Soil moisture, lime, and irradiance produced significant responses in *M. struthiopteris*. Soil moisture had the greatest effect. The significant reduction in fresh and dry weights of both frond types at low soil moisture indicates that this is the major factor limiting distribution to habitats with a constant water supply as previously

Table VI. Comparison of vegetative fronds on infertile plants, vegetative fronds on fertile plants, and fertile fronds. Number in brackets is the sample size.

Parameter	Vegetative fronds on sterile plants (Mean ± SE)	Vegetative fronds on fertile plants (Mean ± SE)	Fertile fronds (Mean ± SE)
Fresh wt (g/plant)	127.00 ± 9.15 (34)	171.66 ± 19.27 (14)	15.62 ± 3.49 (14)
Dry wt (g/plant)	22.58 ± 1.53 (34)	36.67 ± 3.95 (14)	2.44 ± .58 (14)
Nitrogen (%)	1.84 ± .06 (34)	1.35 ± .07 (14)	2.18 ± .13 (12)
Potassium (%)	1.41 ± .06 (34)	1.14 ± .09 (14)	2.03 ± .04 (11)
Phosphorus (%)	0.27 ± .01 (34)	0.20 ± .02 (14)	0.38 ± .02 (12)
Calcium (%)	1.13 ± .03 (34)	1.17 ± .04 (14)	0.16 ± .01 (12)
Magnesium (%)	0.17 ± .01 (34)	0.16 ± .01 (14)	0.20 ± .01 (11)

Table VII. Production of a second set of fronds from the original plants, and production of new plants.

	Irradiance (μmol $m^{-2}s^{-1}$)					
	160			418		
	Lime (g kg^{-1})			Lime (g kg^{-1})		
	0	2	4	0	2	4
Original Plants	2	0	0	8	7	8
New Plants	2	2	4	4	2	1

suggested by Mueller-Dombois (1964) and Porfir'ev (1975). Porfir'ev (1975), in his study of the ostrich fern distribution and ecology in the USSR, stated that *M. struthiopteris*, regardless of its geographical location, was associated with a continuous flow of soil underground water rich in oxygen and minerals. On a 0.1-hectare plot which he studied for 7 years, the dry weight of the above-ground biomass varied from 18.3 to 58.6 g m^{-2} (ca. 3.29 - 18.17 g/plant), depending on soil moisture during the growing season. In the same study the projected cover of each fern, which varied from 0.18 to 0.31 m^2, also depended on soil moisture.

Frond height had a positive response to soil moisture and a negative response to irradiance. Difference in height with irradiance is typical of leaves in shade and sun (Boardman 1977; Hariri & Brangeon 1977). In the fern *Pteris cretica*, increasing irradiance was related to increased dry matter per unit surface area, reduced leaf water content, and thicker leaves (Hariri & Brangeon 1977). As the difference in leaf height could not be related to reduction in total frond dry weight in my experiment, higher irradiance probably would not increase frond production, and would probably reduce the height even more. This reduction in height has been observed in plants transplanted to a field plot at the Nova Scotia Agricultural College in which the plants were not shaded.

Even though none of the treatments resulted in any significant difference in the number of fronds produced during the experiment, the number of plants producing a second set of fronds (Table VII) was increased at higher irradiance. This is similar to my observations on the field plot at the Nova Scotia Agricultural College where plants growing in full sun during the first year produced more fronds per plant in the second year.

Soil pH, which was altered by the amount of lime added, could be the explanation for significant differences in the foliar mineral concentrations with lime level. The effect of liming varied among the elements and always involved an interaction with soil moisture or irradiance.

Higher irradiances tended to decrease concentrations of nutrients such as nitrogen and phosphorus as has been shown for other plants (Boardman 1977). However more research must be done to further understand the mechanisms involved, because irradiance had little effect on potassium and none on calcium contrary to other observations (Boardman 1977)..

The positive effect of low soil moisture on percent nitrogen and phosphorus is noteworthy. As this effect interacted with lime levels, it could result from differences in availability of these nutrients in the soil. This soil-moisture effect was most noticeable at the highest lime level. The lower nutrient concentrations in the high moisture treatment could be partly the result of a "dilution effect" caused by greater carbohydrate production.

The accumulation and depletion of nitrogen, phosphorus and potassium in the fertile and vegetative fronds, respectively, suggests that the production of fertile fronds acted as a strong sink, translocating a portion of these 3 mobile nutrients from the vegetative fronds.

Magnesium, although a mobile ion (Bukovac and Wittwer 1957), may not show a similar difference between fertile and vegetable fronds because its main function is in the chlorophyll molecule and the CO_2-fixing enzyme, ribulose bisphosphate carboxylase, and the fertile fronds are considered to have little, if any, photosynthetic activity.

The production of fertile fronds, which were formed on larger than average plants, was related to high soil moisture perhaps because such conditions would allow sufficient production of carbohydrates in the vegetative fronds to nourish the nonphotosynthetic fertile fronds. The relationship between sufficient carbohydrate production in the vegetative fronds and fertile frond production in *M. struthiopteris* was first suggested by the experiments of Atkinson (1896) and Goebel (1905).

More recent evidence, however, indicates that nitrogen, in addition to carbohydrate, can influence fertile frond production. In cultured fronds of *Todea barbara*, sucrose supplemented with nitrate enhanced fertile frond production (Sussex & Steeves 1958). Harvey and Caponetti (1974), using cultured *Osmunda cinnamomea* leaf primordia, concluded that ammonium and not nitrate was necessary, in the presence of high sucrose concentrations, to induce sporangia. Fertile fronds in this study also accumulated phosphorus and potassium. Therefore, the overall nutritional balance of the fronds is important.

Even though liming had no significant effect on production of vegetative and fertile fronds, the possibility still remains that germination of spores or growth and fertilization of gametophytes requires a calcareous substrate and alkaline soil pH. The pH range of natural sites (Gabrielson 1964) is within the optimum pH for fern spore germination in culture media, which is usually in the range of pH 4.5 to 7.5 (Dyer 1979; Page 1979). Evans and Bozzone (1977; 1978) have shown that in *Pteridium aquilinum* (bracken fern), sperm motility and fertilization in the gametophyte were reduced at pH 5.8 and 4.2, respectively. They were reduced even more by the addition of anions such as sulfate, nitrate, and chloride, which are the dominant anions in precipitation, especially in "acid rain" regions. It is also possible that the apparent preference of *M. struthiopteris* for calcareous soils and soil pH close to neutrality is really due to the greater availability in acid soil of elements such as iron, aluminum, or manganese which could be toxic to *M. struthiopteris* (Hou 1950).

In summary,

1. Of the three variables examined, soil moisture had the greatest effect on the production of vegetative and fertile fronds.
2. Irradiance did not affect frond weights in the first set of fronds but it did influence height and nutrient levels and increased the production of subsequent fronds.
3. Liming had no effect on growth and only indirectly affected nutrient levels through interaction with soil moisture and irradiance.
4. Fertile frond production was associated with treatments which resulted in greater vegetative frond production, suggesting the need for higher carbohydrate levels for fertile frond induction. Fertile fronds also had a nutrient depletion effect on the sterile fronds, resulting in higher concentrations of nitrogen, phosphorus, and potassium in the fertile fronds. Only calcium had a lower concentration in the fertile fronds than in the vegetative fronds.

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STUDIES ON THE TAXONOMY AND DISTRIBUTION OF SPHAGNUM. VIII. REDISCOVERY OF SPHAGNUM MACROPHYLLUM VAR. BURINENSE*

Sphagnum macrophyllum Bernh. var. *burinense* Maass is a very rare peat moss which was described from only a single locality on the Burin Peninsula in Newfoundland (Maass 1967). It has since not been collected anywhere else nor in the type locality itself. In September 1979, the type locality was revisited with a view to collecting the moss for an exsiccata. It was possible to relocate the larger of the two ponds in which the plant had been found, on the basis of the habitat photograph furnished with the description (Maass 1967, Fig 30). However, the ecology of the type locality has been drastically changed by road-building, and *S. macrophyllum* var. *burinense* and some of the accompanying species including *S. pylaesii* have disappeared completely. Even the very competitive species *S. torreyanum*, conspicuously visible from a distance by its strong and green capitula, has become scarce although there was no lack of water. On the contrary, the outlines of the ponds became obscured by flooding after the new highway No. 210 (Fig 1) was built in 1971 at a distance of about 150 m to the southeast of the old highway 11 seen in Figure 30 (loc. cit.). Eutrophication and/or toxic components from the tar of the fresh pavement may have contributed to the disappearance of the peat mosses. On the other hand, an unspoiled system of ponds on the large "blanket bog" northwest from the old highway, not far from the type locality, was found to show a very abundant growth of *S. macrophyllum* var. *burinense*. It grew in most of the ponds shown in Figures 2 to 4. Unfortunately, the variety cannot be distinguished in the field from var. *macrophyllum* when wet, except by microscopic study of the characteristic absence or presence of the sharply outlined row(s) of leaf pores (see illustrations in Maass 1967). However, upon drying, the curled or irregularly twisted leaves of var. *burinense* immediately distinguish the latter from the straight-leaved typical variety.

On the basis of the abundant material now available, it was possible to confirm the absence of pores from most of the hyaline cells (hyalocytes) in the branch leaves of var. *burinense* as a constant character. A few of the shorter cells near the leaf tips may, however, contain a single distinct end pore, and a few of the longer cells in the lower one-third of the leaves may contain up to 4 or 5 indistinct pores or membrane thinnings (as opposed to the always distinct and much more numerous pores of var. *macrophyllum*). In addition, the green cells (chlorocytes) in var. *burinense* tend to be wider than the hyalocytes, while the opposite is true with the typical variety. In var. *burinense* there is also a pronounced tendency for the replacement of hyalocytes of chlorocytes. This feature, which is common to some aquatic forms of a few *Sphagnum* species, indicates that environmental factors can interfere with the cell polarity in the very early stages of development, normally resulting in the perfectly regular network of alternating chlorocytes and hyalocytes by which the leaves of *Sphagnum* are characterized. In the dozen or so small ponds in which var. *burinense* was present (Fig 4), it was found either floating around the edges or anchored in the muddy bottom of the ponds down to a depth of 1 m or more. It also grew in a depression (Fig 4e) filled with hydrophilic species of *Sphagnum* identical to those in the ponds (*S. torreyanum, S. cuspidatum, S. pulchrum, S. pylaesii*). None of the material showed any intergradation into var. *macrophyllum*, nor was the typical variety present at all. The typical variety of *S. macrophyllum* has recently been collected in Beaverskin L., Kejimkujik National Park, from a depth of up to 6 m where it formed a lake-bottom carpet along with *S. torreyanum* (Beauchamp 1980).

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*NRCC 18618

Twisted branch leaves combined with a severe reduction of leaf porosity are characteristics of a number of varieties that have been described for seemingly unrelated species of *Sphagnum* belonging to the *Cuspidata* and *Subsecunda* groups. The most famous case is probably *S. annulatum* H. Lindb. var. *annulatum*, the "normal" variety of this taxon being *S. annulatum* var. *porosum* (Schlieph.) Maass & Isoviita (also known as *S. jensenii* Warnst.). In this and similar cases it is not possible to recognize the normal and aberrant varieties in the field while the mosses are wet. As the flexuose varieties are generally very rare but tend to occur in mixed colonies together with their respective "normal" analogue, it is interesting to speculate that they represent a pathological condition and perhaps owe their existence to viral or microbial infections. As viruses have never been detected in mosses, an effort will be made to examine *S. macrophyllum* var. *burinense* for their possible presence. Evidence for a pathological origin of the flexuose varieties of *Sphagnum* would have consequences on their taxonomical status. For instance, *S. annulatum* and *S. jensenii* could not be treated as separate species as has been adopted by Andrus and Vitt (1979). Studies along these lines have been planned in collaboration with Dr. Guy Brassard of Memorial University of Newfoundland.

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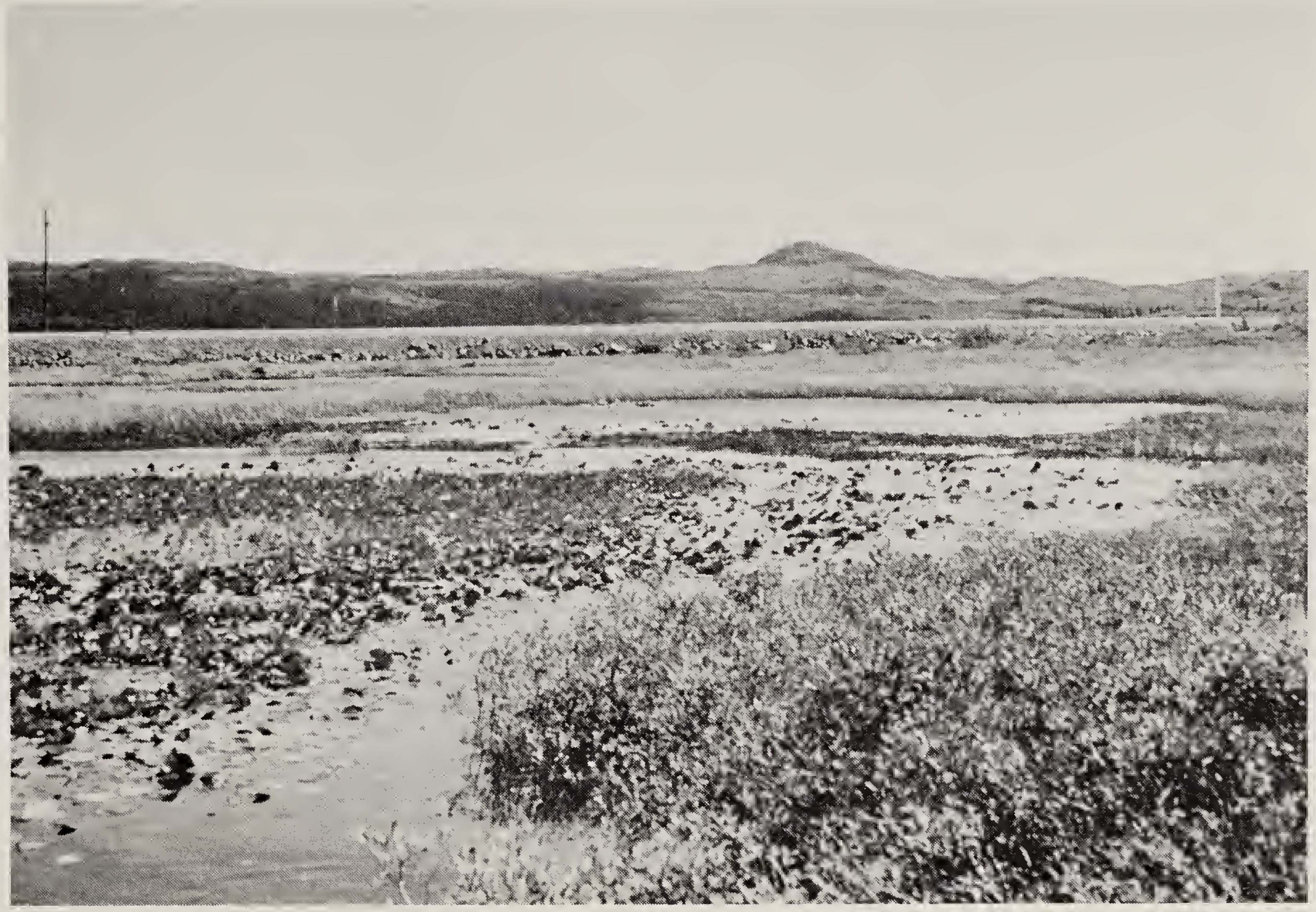

Fig 1. The type locality of *Sphagnum macrophyllum* var. *burinense*, photographed in a southerly direction from the same spot from which Figure 30 in Maass (1967) was taken. In the background is the new highway, the building of which caused changes of the water level and water chemistry and the disappearance of the *Sphagnum* community originally present.

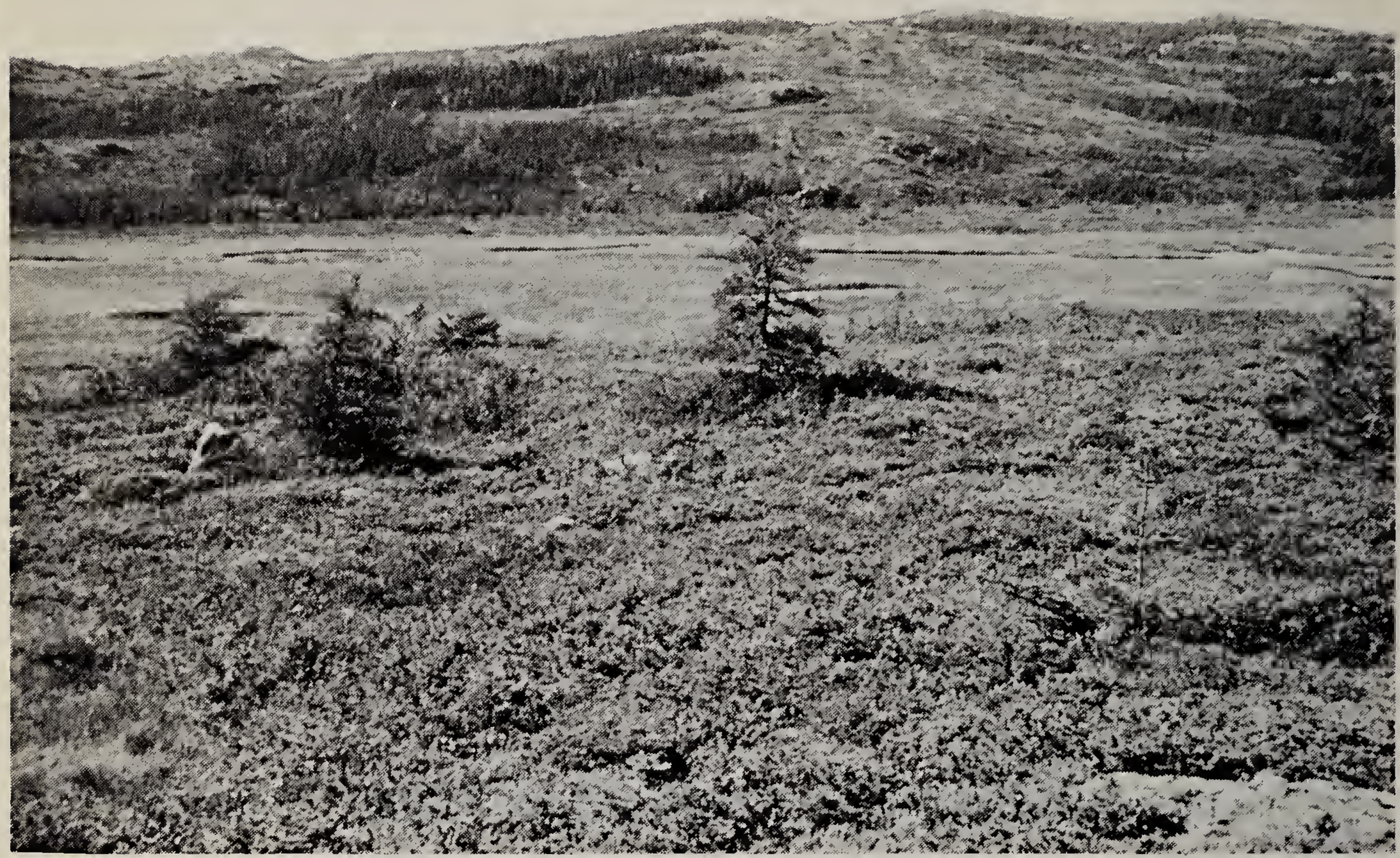

Fig 2. View of the blanket bog (in the middle ground) in a northwesterly direction from near the old road. All of the pools shown in this picture were found to contain *S. macrophyllum* var. *burinense*.

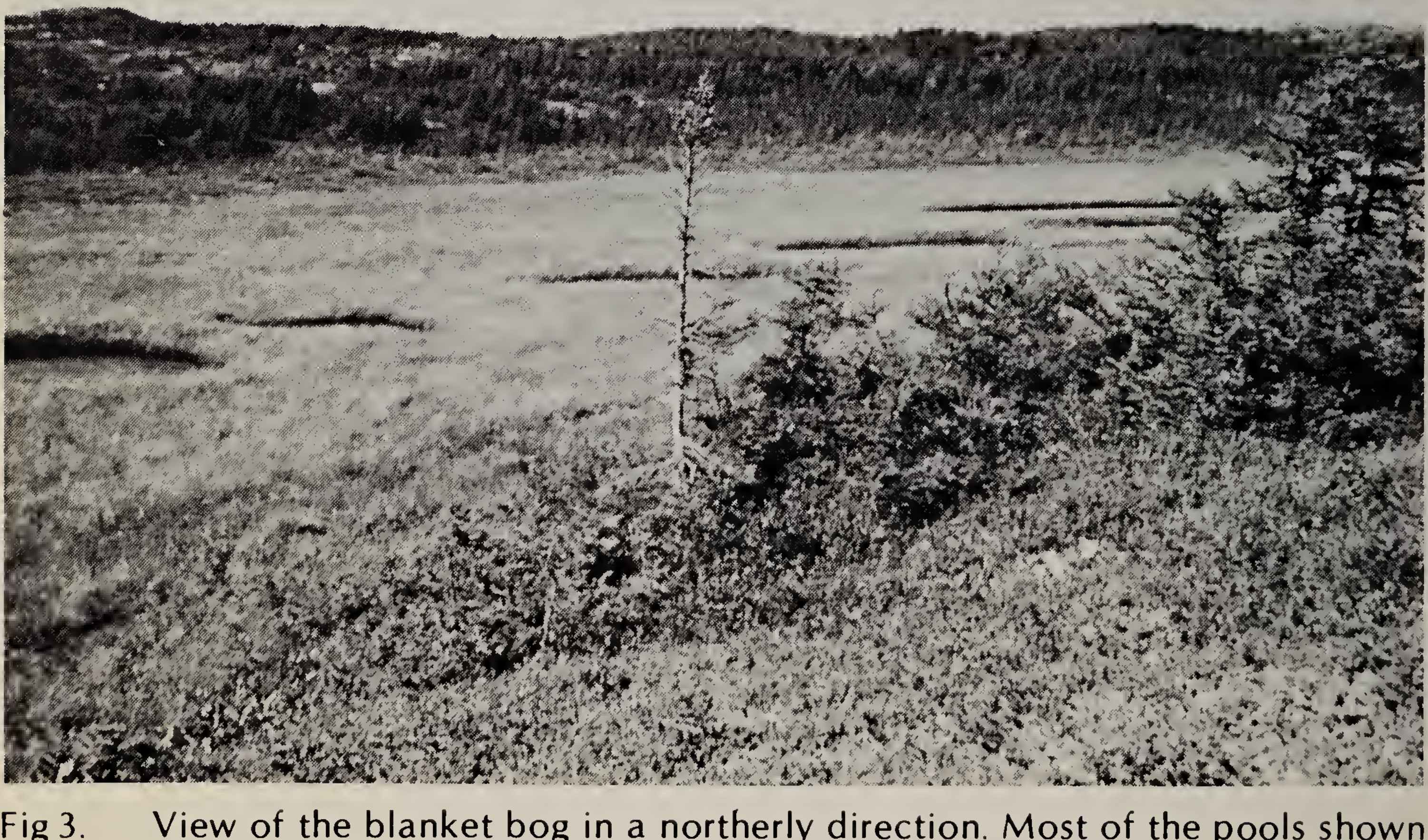

Fig 3. View of the blanket bog in a northerly direction. Most of the pools shown here were found to contain *S. macrophyllum* var. *burinense*.

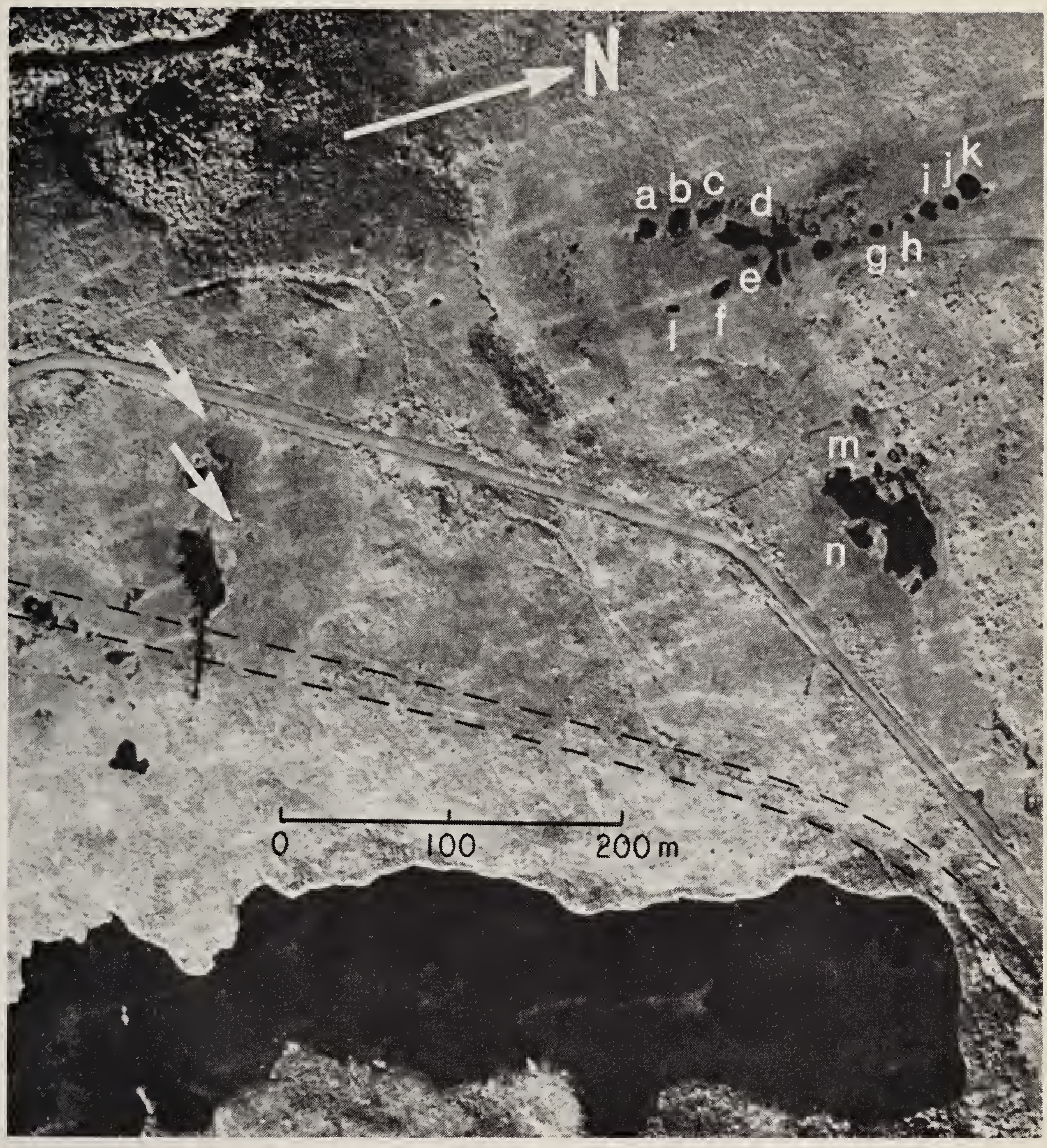

Fig 4. The presently known distribution of *Sphagnum macrophyllum* var. *burinense*. The lower case letters refer to collections from bog pools and bog ponds or wet depressions (e) which have been deposited at NFLD (duplicates of d and e are also at CANM and those of e and n in herb. Maass). Ponds m and n are on higher ground outside of the blanket bog and contained no more than one or two gametophytes each. In this aerial photograph of 1969, the original ponds of the type locality were still recognizable although completely filled in with vegetation (short arows). The old dirt road (Hwy. 11) is clearly visible, and the approximate location of the tar road constructed in 1971 (Hwy. 210) has been indicated by broken lines. The present and former habitats of *S. macrophyllum* var. *burinense* all lie between 75-90 m elevation.

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FIRST RECORD OF FEMALE GAMETOPHYTES OF BONNEMAISONIA HAMIFERA HARIOT (RHODOPHYTA, NEMALIALES) IN NOVA SCOTIA*

The occurrence of female gametophytes of *Bonnemaisonia hamifera* on the coast of Nova Scotia is reported for the first time. Plants with abundant carpogonia and rudimentary pericarps but with no development of carposporangia were located at 4.5 m below mean sea level off Bon Portage Island, Shelburne County on 4 August 1977 (NRCC 6842), and in the drift at Lawrencetown Beach, Halifax County on 7-21 October 1978 (NRCC 8416, 8417, 8419). Hitherto, all collections of reproductively mature *B. hamifera* gametophytes from the Maritime Provinces had been male (Chen et al. 1969; in herb. NRCC), and this observation was reinforced in culture studies wherein germination of tetraspores from *"Trailliella"* populations in this area yielded only male plants (Chen et al. 1969). Pericarps in the Nova Scotian collections were small, reaching only 450-610 x 380-475 μm, as opposed to the normal diameter of 2 mm (Dixon & Irvine 1977), but otherwise were structurally normal (Kylin 1956). The Lawrencetown collection is also noteworthy for the large quantity of material adrift in good condition in the shallows, as previous collections of gametophytes suggested this phase to be very meagre in our waters.

Since the discovery of *B. hamifera* in Europe near the end of the nineteenth century (Batters 1896; Buffham 1896), the life history of this alga in the North Atlantic has been problematical. Various anomalies in the observed distribution and fertility of both the tetrasporangial and gametangial phases (e.g., Kornmann & Sahling 1962; 1977) have led to the suggestion that propagation and dispersal are primarily by vegetative means instead of by the normal sequence of generations (Chemin 1929; Dixon & Irvine 1977). Additionally, developmental peculiarities in culture (Chen et al. 1969; 1970; Kornmann & Sahling 1962) suggest parasexuality in this species, and it has been speculated that sex may not be determined genetically (Bichard-Bréaud & Floc'h 1966). The absence of carposporophytes in the Nova Scotian material is consistent with reports of infertile pericarps in Massachusetts (Taylor 1957), where male plants of *B. hamifera* have not yet been reported. Given the previous incidence of males in Nova Scotian waters, however, it is interesting that fertilization was not effected in the present instances.

Simon-Bichard-Bréaud (1970) contends, on the basis of a study of herbarium specimens, that a normal sequence of gametangial, carposporangial and tetrasporangial phases in fact does occur on both sides of the North Atlantic, and that plants with sterile pericarps are merely females that continue to issue carpogonia after the disappearance of spermatangial branches. Although this view has not been universally accepted (e.g., Dixon & Irvine 1977), it should be pointed out that fertile males have been observed in Nova Scotia only in February (Chen et al. 1969; in herb. NRCC), and the females under consideration here were collected after the major incidence of fertile cystocarps, May to July, reported by Simon-Bichard-Bréaud for North Atlantic material [but see Hehre and Mathieson (1970) for records of only infertile gametophytes in April, June and July in New Hampshire]. Thus, it is conceivable that fertile male plants were extremely rare during 1977-1978, or at least isolated geographically or temporally from the females in question. The complete absence of larger, functional cystocarps emptied of carpospores, on the lower portions of the plants (c.f. Kornmann & Sahling 1961, in Helgoland) indicates that production of carpogonia occurred entirely in the absence of spermatia. Moreover, the Lawrencetown collection, though large, was wholly female and may well have been fragments of a large clone rather than a number of individuals from a disproportionately female community. Unfortunately, the collections were preserved in formalin before their female nature was recognized, and efforts to locate similar plants for study in culture have been limited and unsuccessful.

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*NRCC No. 18619

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PROC. N.S. INST. SCI. (1980)
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Pterycombus brama was not listed for the Atlantic coast of Canada by Leim and Scott (1966) or Legendre (1978). However, Mead (1972) listed one specimen for the Grand Banks which he described as " . . . archaic, eviscerated, twisted, frayed, broken and generally . . . distorted . . . ". Our specimen, from about 1000 km westwards, is happily in better condition, the only damage being several splits in the membranes at the vertical fins and a milkiness of the cornea, presumably due to a day's delay in preservation. The specimen is catalogued as NMC80-1115 in the National Museum of Natural Sciences, National Museums of Canada, Ottawa.

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Poisson-éventail atlantique

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Body elongate, compressed, greatest depth 2.7 (2.1-2.5) in standard length at base of pectoral fin; caudal peduncle slender. Head compressed, short, length 4.1 (3.5-4.2) in standard length; profile of underside curving into thorax, dorsal profile straight to dorsal fin. Mouth superior, almost vertical, 70° to horizontal axis; slender pointed teeth in jaws. Orbit large, horizontal diameter 3.2 (2.6-3.2) in head length. Fins: dorsal (1) 51 (48-53), very high anteriorly, equalling body depth, fin begins just behind orbit and ends on caudal peduncle; caudal deeply forked; anal 42 (40-42), resembling dorsal fin; pelvics small, 15; pectoral 19 (20-23), elongate, length exceeds head length. Scales large, 51 (48-53) in median longitudinal series, without lateral line canal in adults; enlarged scales form sheaths at bases of dorsal and anal fins. Scales cross body in front of dorsal fin. Vertebrae 48. Colour, bright silvery body in life; dorsal and pelvic fins black.

Distinctions

The great fan-like dorsal and anal fins distinguish the Atlantic fanfish from the other Canadian members of the family and all other species in the region.

Size

Our specimen is 183 mm in standard and 229 mm in total length; the species reaches 368 mm in standard length.

Range

From Jamaica north to Grand Banks including the Sargasso Sea in western North Atlantic, from off Spanish Sahara and off Spain, off northern Scotland to northern Norway in the eastern North Atlantic.

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One specimen recorded previously from about the center of the Grand Banks (Mead, 1972). Our specimen is from Taylors Head area, Halifax County, Nova Scotia.

Biology and economics

Probably spawns throughout the year near the edge of the continental shelf off the east coast of Florida, in the Gulf Stream and adjacent parts of the Caribbean and Gulf of Mexico. The young seem to occur randomly between 25 and 300 m. One or two adults are caught in each winter longline set, in the *Brama brama* fishery off Spain.

Some small differences in counts and measurements between our specimen and Mead's (1972) description can probably be attributed to the small sample size; Mead had only 8 adult specimens available for study material.

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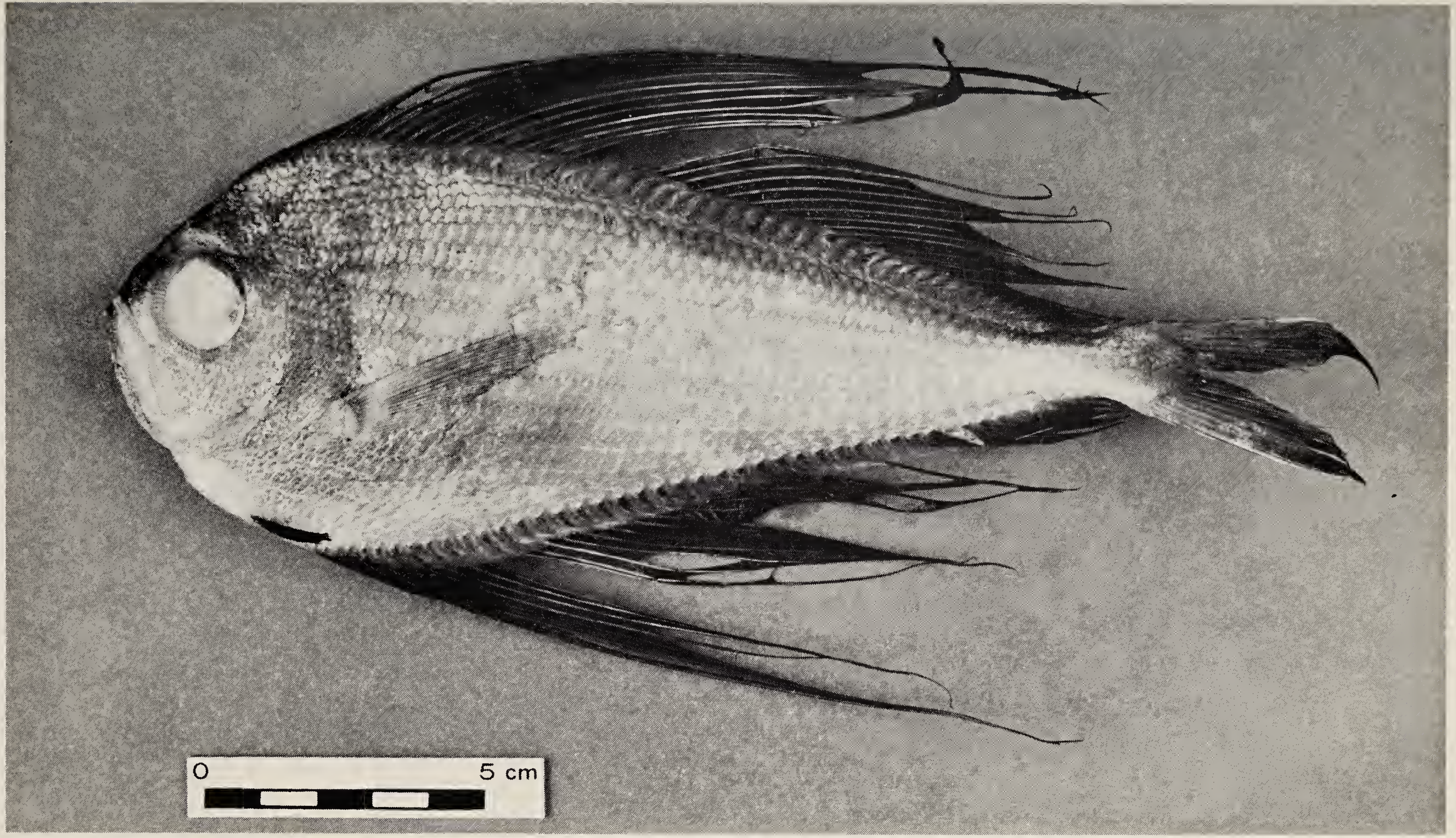

Fig 1. Atlantic fanfish, *Pterycombus brama*, from near Taylors Head, Halifax County (44°48′N, 62°34′ W), captured on August 10, 1980. This specimen, NMC80-1115, represents the first Nova Scotian and second Canadian record of the species. National Museums of Canada, Photographic Div., Neg. No. AC-30-80-1.

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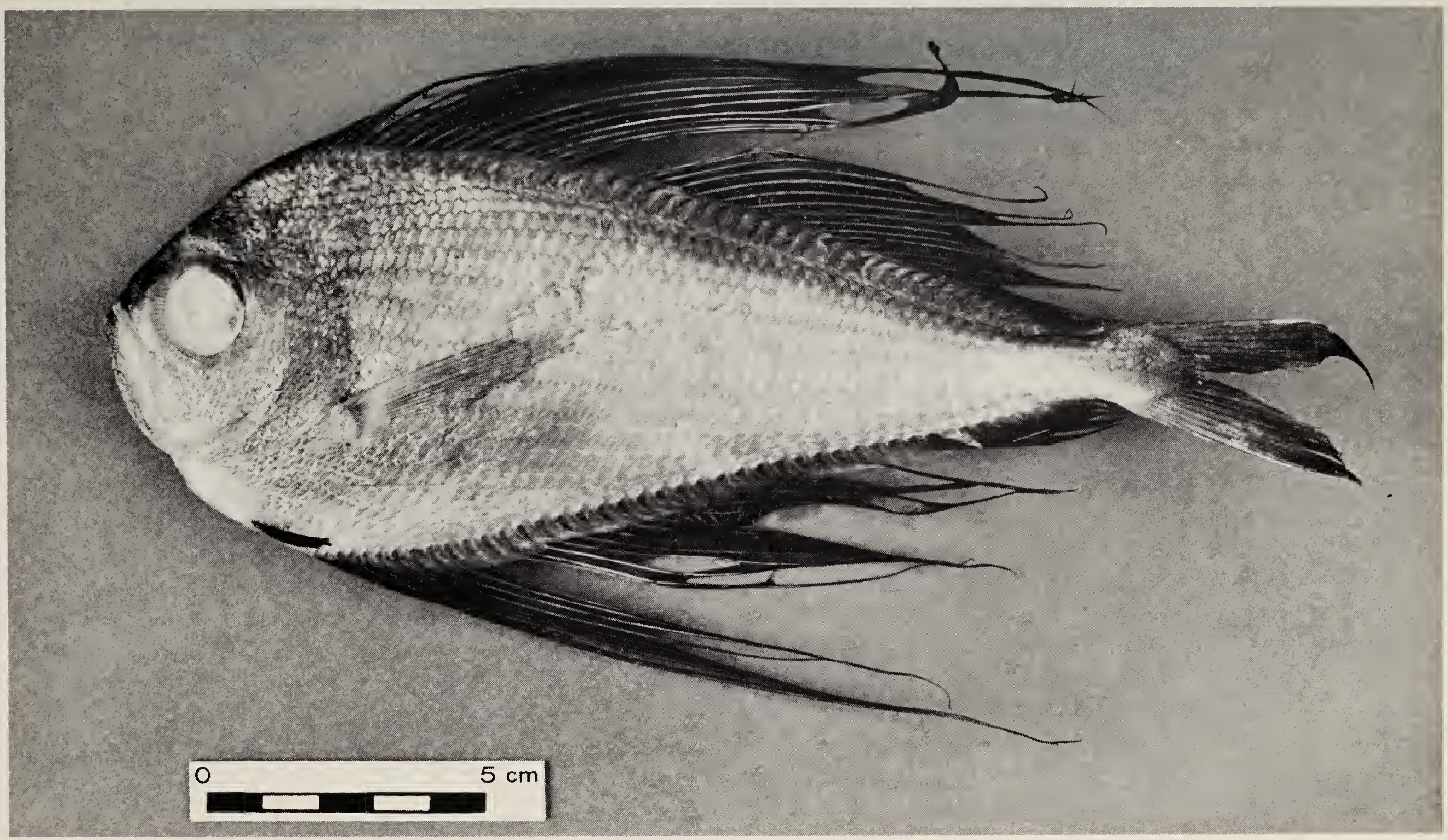

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